Bread and durum wheat performance under a wide range of environmental conditions

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“Then the woman said, Enkidu, eat bread, it is the staff of life”

The Epic of Gilgamesh, *c*. 4100 BP.

To

Marcel;

my wife, parents, brother, goddaughter and family;

my friends.

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Abstract

It has been assumed that durum wheat is more productive under stress than bread wheat (geographical distribution and statements in the literature). However, this is not known as only few research papers compared the performance of both crops, and in no case under a wide range of environments in field conditions. This study did precisely this sort of comparison, along 3 experimental years in which a range of fertilization and irrigation treatments were applied. In addition, a comprehensive database with data from field experiments was gathered and meta-analysed. We found from both approaches a cross-over interaction of yield of bread and durum wheat, but rejecting the hypothesis: bread outyielded durum wheat in the low-yielding conditions while durum wheat tended to have higher yield potential as a consequence of differences in sink strength in post-anthesis. The causes under the yield interaction and its consequences in efficiency terms are discussed.

Resumen

Se acepta comúnmente que los trigos duros son más productivos que los trigos harineros en ambientes de estrés (en su distribución geográfica y en la literatura). Sin embargo, dicha asunción no está plenamente demostrada dados los pocos artículos científicos que comparan el comportamiento de ambas especies en condiciones de campo, que en ningún caso presentan un amplio rango ambiental. Este estudio evaluó dicha comparación a lo largo de 3 años experimentales en los que se aplicó un amplio rango de condiciones de fertilización y riego. Adicionalmente, se realizó una exhaustiva base de datos de experimentos que fue meta-analizada. Se encontró con ambas aproximaciones una interacción de tipo cualitativa del rendimiento entre ambas especies con el ambiente, aunque rechazando la hipótesis original: el rendimiento del trigo harinero fue mayor que el del trigo duro en los ambientes con bajo rendimiento y, al contrario, el trigo duro tendió a expresar un rendimiento potencial más alto como consecuencia de diferencias en la fuerza de los destinos en pos-antesis. Las causas subyacentes en la interacción del rendimiento y sus consecuencias en términos de eficiencia han sido ampliamente tratadas.

Resum

Els blats durs han estat àmpliament acceptats com a més productius en ambients d'estrès que els blats fariners (en la seva distribució geogràfica i en la literatura). Tanmateix, l'esmentada assumpció no està plenament demostrada a causa dels pocs articles científics que comparen el comportament de ambdues espècies en condicions de camp, que en cap cas presenten un ampli rang ambiental. Aquest estudi avaluà la dita comparació durant 3 anys experimentals en els quals un ampli rang de condicions de fertilització i reg varen ser aplicats. Addicionalment, es realitzà una exhaustiva base de dades de experiments que fou meta-analitzada. Totes dues aproximacions presentaren una interacció amb l'ambient de tipus qualitatiu del rendiment entre les dues especies de blat, encara que rebutjant la hipòtesis original: el blat fariner va rendir més que el blat dur en els ambients de baix rendiment i, contràriament, el blat dur va tendir a expressar un rendiment potencial més alt a conseqüència de diferències en la força dels destins en post-antesis. Les causes que produïren la interacció del rendiment i les conseqüències en termes d'eficiència han estat àmpliament estudiades.

Chapter I: General Introduction

Abstract

Wheat is among the most relevant cereals for humanity, who from the early beginning of the agriculture has been selecting the plant to suit his needs. Bread wheat (*Triticum aestivum* L.), which is the largest cultivated of the wheat species, is widely spread and adapted to almost all the temperate zones of the world, in contrast to durum wheat (*Triticum turgidum* L. ssp. *durum*), which is the second largest cultivated wheat species, about a 6% of the total, and is mainly distributed along the Mediterranean Basin. Since both species have a similar role, its tendencies of consumption are dynamic and share similar environmental niches; they could be largely interchangeable. However, it is frequently assumed that durum wheat is more adapted to stress than bread wheat, in association with its particular distribution (durum wheat generally in lower-yielding environments). Unfortunately, few research papers compare the performance of both species grown side-by-side under a wide range of environments in field conditions and is not known if the rationale behind the different distribution is related to their relative performance under particular yielding conditions, or rather to historical and cultural terms. In the present thesis, I aimed to compare durum and bread wheat performance under field conditions for a wide range of environments; which is highly convenient to ensure food security, rationalize land use, and learning from the problable differences in adaptation and yield between the wheat species. A general description of yield, its components and the previous knowledge in the relative species differences in performance and the outline of the thesis are provided.

Keywords: Triticum, wheat, origin, distribution, yield, adaptation.

1. Wheat origin, importance and future perspectives

Wheat (different species of *Triticum*), among other cereals, was consumed by humans before the beginning of agriculture. Nonetheless, from that moment on, the intuitive process of picking the biggest grains for sowing the next crop progressively changed those regular grasses to suit human needs, starting an approach to a plant ideotype with better agronomic characteristics, including higher yields (Fig. 1). That first "green revolution" for wheat started along the Fertile Crescent *c*. 10,000 BP (Hillman and Davies, 1990) with the progressive domestication of some species of wheat, remarkably the eikorn (*Triticum monococum*) and the emmer wheats (*Triticum turgidum* ssp. *Dicoccum*) which were widely used in the ancient times (Mac Key, 2005) and from which in some moment the modern bread and durum wheats derivate. The cultivated emmer has a lower TKW (thousand kernel weight) than durum (Faris *et al*., 2014) and bread wheat (Konvalina *et al*., 2008) is hulled and do not contain the Q "domestication" gene related to the pleiotropic effects of free threshability, rachis stiffness, and glumes tenacity. Durum wheat, (*Triticum turgidum* L. ssp. *durum*) shares the AABB genome with its ancestor, while the hexaploid bread wheat (*Triticum aestivum* L.) with the AABBDD genome derivates by a process of allopolyploidization from the tetraploid emmer and the D genome from the wild diploid *Triticum tauschii* (Coss.) (Huang *et al*., 2002; Marcussen *et al*., 2014) (Fig. 1), an annual grass which usually produces numerous tillers, thin stems, small and narrow leaves, and small grains (Ehdaie and Waines, 2013). Despite that it is controversial the exact timing when bread wheat allopolyploidization occurred, it must have been relatively recent, since the Q gene found in both wheat was originated from a single event in the past (Simons *et al*., 2006). That additional ploidy level conferred to bread wheat a greater adaptability and numerous loci for constrain resistance have been found on it (Mujeeb-Kazi and Hettel, 1995).

Wheat is one of the most important cereals feeding humanity (Shewry, 2009), nowadays 7000 millions of people. Nonetheless, with the latest estimations concerns are growing about the possibility that food production will not meet demand in some near future (Pinstrup-Andersen *et al*., 1999; Tweeten and Thompson, 2009; FAO, 2009; Godfray *et al*., 2010; Reynolds *et al*., 2012; Keating *et al*. 2014), since by the 2050 the humanity will have reached 9.1 billion, the food production must increase about a 70 % (FAO, 2009) or up to 98% considering the higher socioeconomic development expected (Valin *et al*., 2014). Following that considerations Borlaug, 2002 calculated *c*. a 57% by the year 2025; which for wheat means that world average yield must increase at a rate of *c*. 70 kg/ha per year (Fig. 2). However, increases in food production (Alexandratos, 1999; Borlaug, 2002) and in wheat yield potential are diminishing (Traxler *et al*., 1995; Acreche *et al*., 2008; Graybosch and Peterson, 2010; Fischer and Edmeades, 2010; Sanchez-Garcia *et al*., 2013), a fact observable as an apparent slowing of yield increases around the decade of the 1990's (Fig. 2a) and that the world cultivated area apparently reached an upper limit of *c.* 5 Gha.

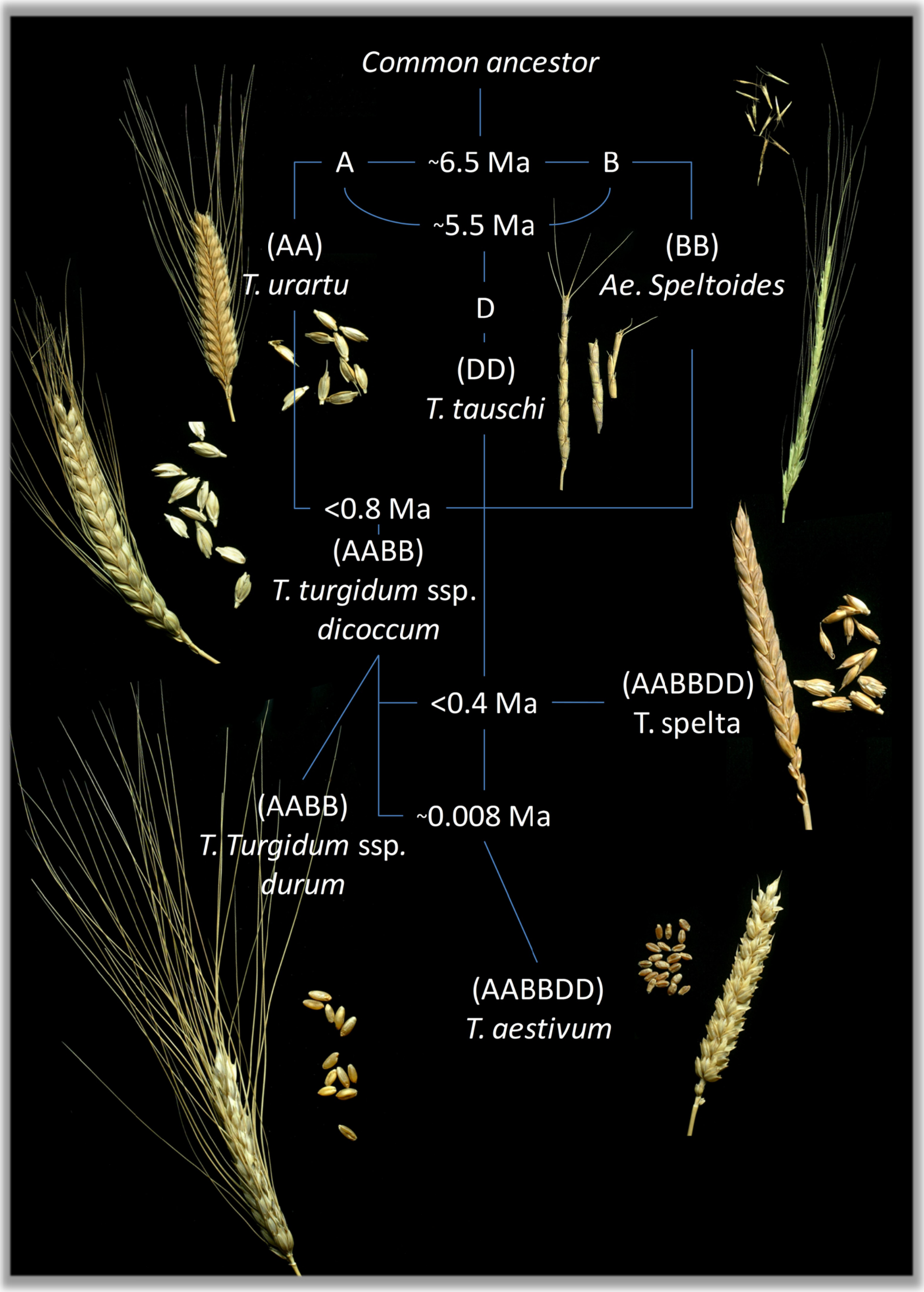

Figure 1. Model of the phylogenetic history of bread and durum wheat, with the approximate dates for divergence and hybridization events. Adapted from Shewry (2009) and Marcusen *et al*., (2014). Images available at http://www.sortengarten.ethz.ch.

Those predictions are controversial because other authors postulate a decrease in human fertility (Alexandratos, 1999; Johnson, 1997; Bongaarts, 1996; FAO, 2009) (Fig. 2d) and others the steadily increase of yield potential (*e.g.* Nalley *et al*., 2010; FAO, 2009).

Furthermore, less than a half of the amount of cereals produced is consumed as food (Fig. 2b); and therefore restructuring cereals end use, *i.e.* to increase cereals direct consumption, could maintain a higher human population. Moreover, the fact that the cereals cultivation area is not limited by the plateau achieved in the total agricultural area, suggests that nowadays production is more limited by price than by land availability, and that is why still there is some room to increase cereal production via increasing the area when the prices and demand increases.

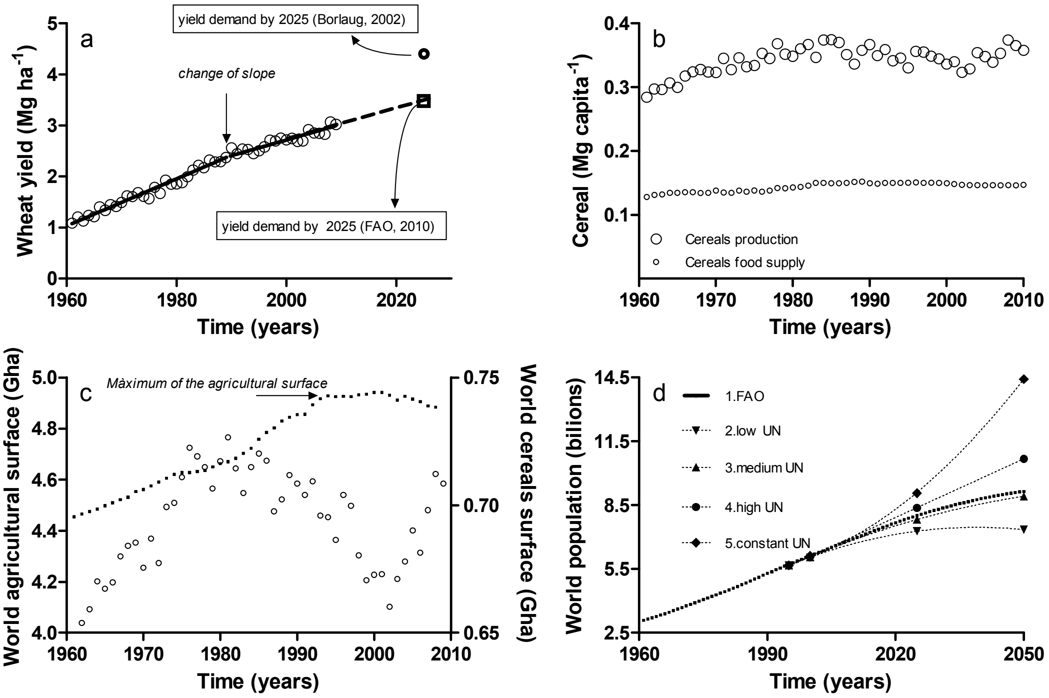

Figure 2. World average wheat yield (circles) and forecast of yield to meet demand in 2025 (dashed line) a), World cereals production per heat b), Agricultural surface (doted line) and cereal surface (circles) in the world c), World human population and plausible future scenarios: 1.FAO and UN, 2. Low fertility 0.5 descendents per woman, 3. Medium fertility 2 descendents per woman, 4. High fertility 2.5 sons per woman, 5. Constant fertility or maintaining nowadays fertility d). Data obtained from FAO (www.fao.org) and UN (www.un.org).

Nonetheless, climate change and the overuse of resources can potentially worsen dramatically the situation (Wheeler and von Braun, 2013), global rises by up to 2.2 ºC degrees are expected by the half of this century (IPCC, 2014) wile direct yield losses of between a 2.5 to 16% are calculated for every 1ºC of increase in seasonal temperature (Battisti and Naylor, 2009); water drought events will double by the middle of this century (Sheffield and Wood, 2008), and an increase of a 20% of irrigation water demand is estimated to be needed in order to maintain the current irrigated areas (Wada *et al.*, 2013). Additionally, N is expected to be less available due to rises in the costs of fertilizers, related to the expected rises in petrol prices (Abas *et al.*, 2015), and because governmental policies will restrict N use (Winiwarter and Hettelingh, 2011) as a consequence of its important role in the global warming and in polluting the waters (Vitousek, 1994; Pinder *et al.*, 2012). In this context, an effort should be made in raising yield and adaptation of field crops, particularly with the focus to increase the efficiency in the use of resources of the staple cereals.

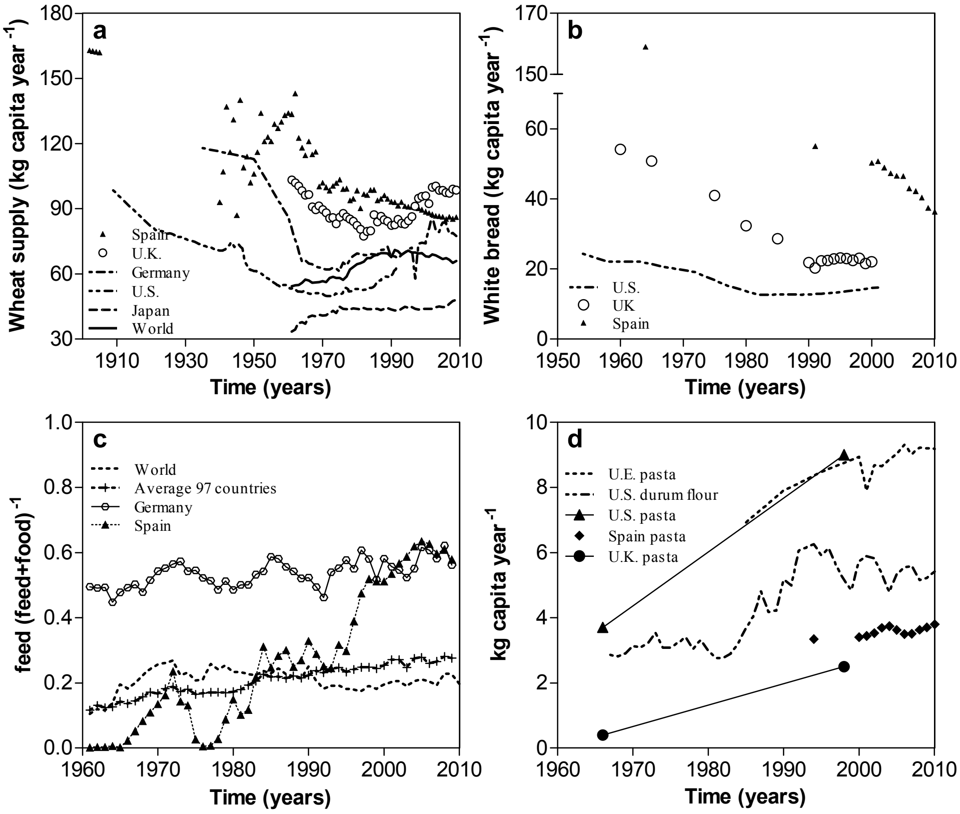

Figure 3. Total food wheat supply by year a), white bread supply by year b), proportion of feed vs. the total food and feed supplied by year c), pasta consumption per capita by year d). Data obtained from FAO (www.fao.org), Cussó and Garrabou, 2007, the Spanish agriculture ministry (http://www.magrama.gob.es), the UK agriculture ministry (www.gov.uk/) and the USDA (www.usda.gov).

2. Bread and durum wheat relative importance and end uses

World wheat production is *c*. 644 millions of tones, most of them from bread wheat, which is one of the most important staple foods of the human diet, providing *c*. 19% of the carbohydrates and 20% of proteins (Braun *et al*., 2010) by direct consumption. What is more, in some countries wheat consumption can reach the 63% of the total ingested calories (http://faostat.fao.org/). Even so, cereals and wheat food consumption has been largely decreasing in many countries in the last half of the century, and at global level from the decade of 1990 (Fig. 3a), which is a clear example of the important reduction in bread wheat and other starchy foods consumption which follows economic development (Grigg, 1996). In particular, the traditional consumption of bread wheat, as common white bread, seems to be diminishing steadily in many traditionally bread consuming countries (Fig. 3b), *v.g*. it is paradigmatic the case of Spain, a traditionally large bread consumer, where consumption decreased *c*. 70 % in the last half of the century (Cussó and Garrabou, 2007). Inversely, the amount consumed indirectly as feed for livestock (*c*. 25% of total world wheat production) firmly increased in many developed countries during the last decades (Fig. 3c) as a consequence of an important increase of meat consumption; but expectedly, other end products will particularly be important future sinks of wheat production, *e.g*. biofuel (Shewry, 2009) or bioplastics (Domenek *et al*., 2004).

Durum wheat, in contrary to bread wheat, is a relatively minor crop *c*. 6% of total wheat production (International Wheat Council, 2010), mainly distributed in the Mediterranean basin, which is mostly used for human direct consumption as pasta products, couscous, and flat bread. However, durum wheat consumption has a small but constant tendency to increase in many countries (Fig. 3d), (Taylor and Koo, 2011); as a consequence of increases in pasta products, *e.g*. pasta consumption per capita in 2000 (8.8 kg) almost doubled the consumption in 1975 in the U.S., (Elias and Manthey, 2005), and because the popularization of new durum products (*e.g*. couscus, flat bread and kebab double-sided bread) (Elias and Manthey, 2005; Sissons, 2008).

Overall, it is important to remark that wheat consumption habits and uses are changing and despite most wheat production is used for human direct consumption, an important part of the wheat uses can be indistinctly satisfied by both wheat species.

3. Geographical distribution from bread and durum wheat and regional characterization

Bread wheat is the crop most widely grown (Fig. 4a), sown in almost every agricultural region of the globe (Slafer *et al*., 1994), carrying an important genetic pool inherited from its ancestors or generated by the relatively high frequency of mutation that posses making that cereal one of the more plastic (Dubcovsky and Dvorak, 2007), able to overcome the important variety of climatic, geographic or biological constrains like: water scarcity, waterlogging, salinity, cold and heat conditions, poor nutrient soils, pests and diseases among others. In contrast, durum wheat is a cereal grown in a more restricted range of agricultural regions, noticeably in the Mediterranean basin which accounts for more than a half of the worldwide durum wheat growing area (International Grains Council, 2010), (Fig. 4b). The Mediterranean climate, *c*. 10% of the wheat growing area, is characterized by having constitutive stresses affecting rather critically, dryland cereal yield, the most important of them are water and high-temperature stresses, which are combined in time, normally during the terminal part of the growing season (Loss and Siddique, 1994), which commonly affects cereal grains filling capacity. The dry season can last between 1 to 8 months and rainfalls, commonly less than 500 mm year^{-1} (Acevedo *et al*., 1999), occur erratically from winter to spring.

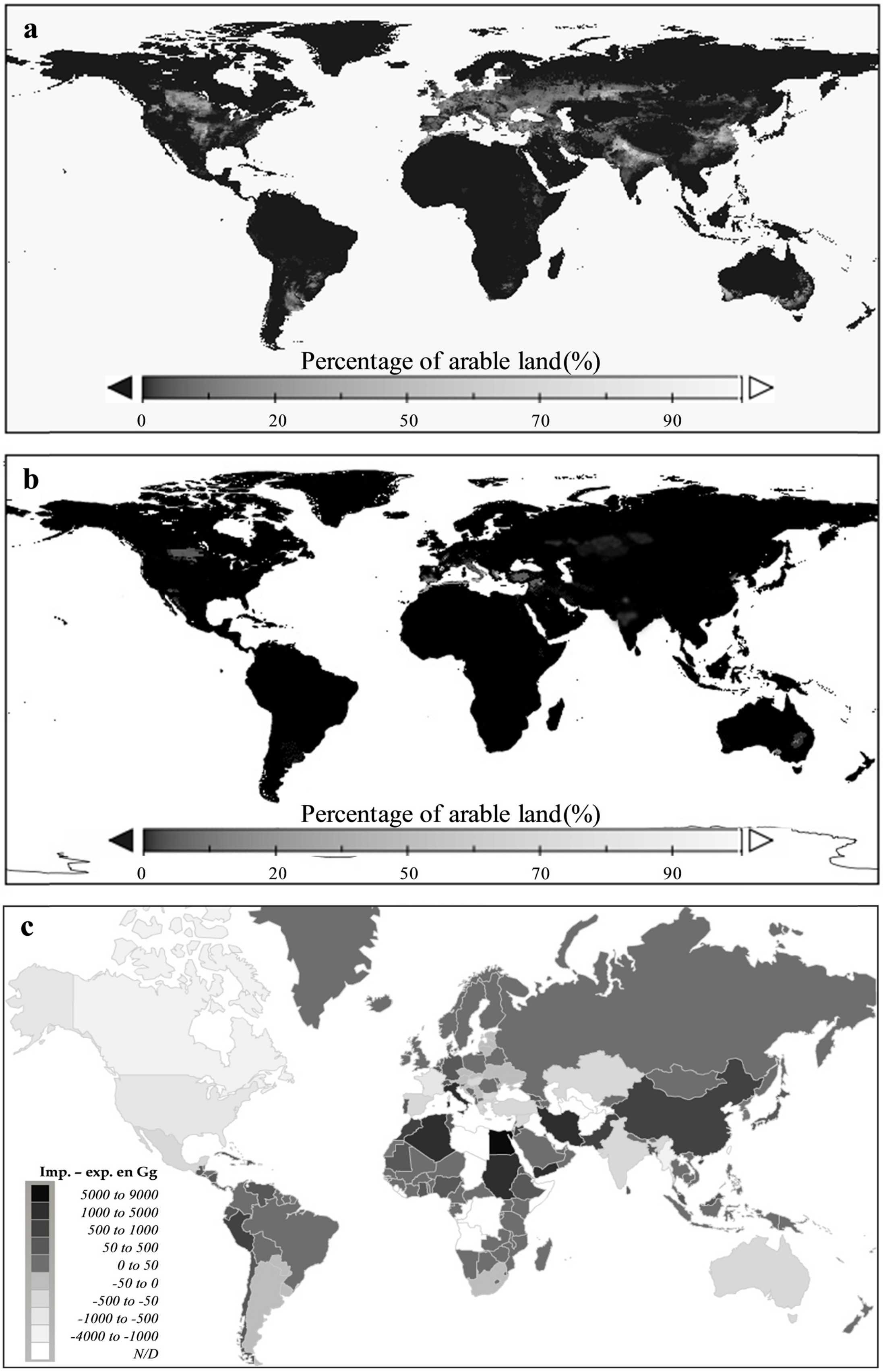

Figure 4. Bread wheat surface from total arable land, adapted from Monfreda *et al*., (2008) a), Durum wheat surface from total arable land, adapted from USDA (http://www.ers.usda.gov/) b), Durum wheat importations minus exportations for the period (2000-2008), adapted from UN (http://comtrade.un.org.) c).

In the Mediterranean basin, where both bread and durum wheat are sown (proportions depending on each particular country), it has been traditional to grow durum wheat and barley in the lower-yielding (< 450mm year^{-1}) conditions and bread wheat in relatively in less stressful conditions (Ceccarelli *et al*. 1987; Acevedo, 1991). Furthermore, in other regions of the world, as the Southern Prairies (Canada), North Dakota (USA) or the southern part of the Buenos Aires province (Argentina) durum wheat is also grown in relatively lower-yielding conditions than bread wheat. Perhaps due to its particular distribution, durum wheat production is associated with relative good yields under low-yielding conditions (Percival, 1921; Bozzini, 1988; López-Castañeda and Richards, 1994; Trethowan *et al*., 2001; Elias and Manthey, 2005; Monneveux *et al*., 2012; Morris *et al*., 2015). The other reasoning behind its particular allocation in lower-yielding conditions may be its requirement of relatively high protein content together with the empiric evidences of negative relationships between yield and protein percentage (Kibite and Evans, 1984). However, as the requirements of a high protein can also be achieved under high-yielding irrigated conditions, with the adequate fertilization and genotype (*e.g*. Abad *et al*., 2004; Rharrabti *et al*., 2001), the main reason must have been the assumption of durum wheat being more tolerant to stresses and bread wheat higher-yielding in stress-alleviated conditions.

The reasoning behind the differential bread-durum cultivation pattern is strong enough in order that many countries which export large quantities of bread wheat, to import large quantities of durum wheat to satisfy their internal demand, *e.g*. EU, Russia, Egypt, China. And on the contrary, some durum producing countries, with low-yielding agricultural areas to be net bread wheat importers wile exporting large quantities of durum wheat *e.g*. Syria, Turkey, Greece (Fig. 4c).

Harlan (1981), based on the cereal species distribution, the archaeological and historical evidences, assumed that the great expansion of raised breads would be a consequence of the Roman Empire acceptation of the product and conversion of their conquered lands to supply Rome, meanwhile durum wheat would had a more Mediterranean limited expansion (Harlan, 1981; Moragues *et al*., 2006).

The rationale behind the land pattern allocation among species is relevant as prioritization of the more adapted species to particular niches, as it may allow improvements in nutrients use efficiency and consequently contributing to increase economic and environmental sustainability.

The Mediterranean climate, with high climatic variability, is an ideal background to test the assumptions made with experiments comparing side-by-side the two types of wheat under contrasting management in the field. Thus, experiments for the present thesis were conducted in Agramunt, a typical rainfed agricultural system within the Mediterranean basin.

Rainfall in Agramunt from 1967 until 2007 was in average 404±139 mm, and remarkably ranged from *c*. 700 to 100 mm while tended to diminish in the locality during the period (slope = -5.25mm year^{-1}, $P < 0.05$), which is related with the important cyclic and erratic variability along time.

Furthermore, along the period, the average temperature per year was 14ºC. In contrast, between May and June, the months where commonly grain filling takes place in the zone, the average temperature was *c*. 26ºC, with picks of maximum values up to 40ºC.

In addition to the climatic variation between growing seasons, I further expanded the range of yield and environmental conditions achieved with a range of water and nitrogen treatments.

4. Physiological bases of wheat species differential yielding and adaptation to the environment

Yield is the result of complex interactions throughout the growing season with the direct or indirect expression from most of the genes (Slafer, 2003). It is a complex character and any attempt to increase it would be more likely if based on a deep understanding of its generation. Commonly, yield can be divided into its components (Fig. 5), *i.e.* plants m^{-2}, spikes plant^{-1}, spikelets spike^{-1}, grains spikelet^{-1}, and grain weight, we can find evidences that both wheat species differ in some of those variables in the literature (Fischer and Wood, 1979; López-Castañeda and Richards, 1994; Zubaidi *et al*., 1999; Trethowan *et al*., 2001; Reynolds *et al*., 2002).

Unfortunately, differences in some variables, between the studied species or cultivars, are not directly translated to yield, because the existence of competence between plants for resources and because the yield components present relationships of competence between them determining yield components compensations (Fischer, 2001; Slafer, 2003), *e.g*. more spikes m^{-2} implies a lower number of grains spike^{-1}. However, differences in physiological attributes, such as the duration of the crop growth phases, the efficiency in capturing and using resources or in response to stress, can result in actual yield differences, disregarding the compensations that may exist.

The number of grains per unit land area, the component which mostly determines yield (Slafer *et al*., 2014), is generated, from sowing to anthesis, from the components spikes m^{-2} and grain number spike^{-1}. Both components are negatively related when the growing juvenile spikes (where the florets are developing) compete with the elongating stems (Fischer 1983; Kirby, 1988). This critical period largely determines the sink size along grain filling (Slafer *et al*., 1996). As commonly wheat, as many cereals, is sink limited during grain filling (Slafer and Savin, 1994; Borrás *et al*., 2004; Bingham, 2007), sink size have been one of the principal targets of modern breeding by changing the biomass partition to grains or harvest index (HI) (Fisher, 1983; Siddique *et al.*, 1989a; Slafer and Andrade, 1993). Contrastingly, the total biomass barely increased for bread wheat (Austin *et al.*, 1980; Calderini *et al.*, 1995; Sayre *et al.* 1997) or slightly increased as a consequence of improvements in post-anthesis sink strength (Fischer *et al.*, 1981; Reynolds *et al.*, 2007). Breeding for partition has been similar between bread and durum wheat (De Vita *et al.*, 2007; Álvaro *et al.*, 2008).

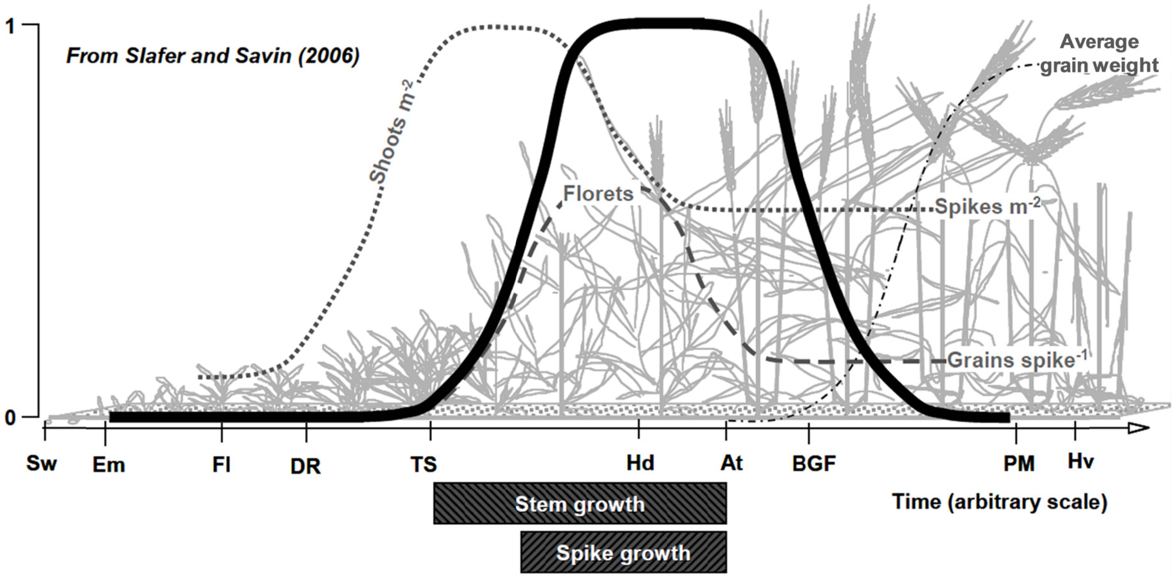

Figure.5. Stages of wheat development: Sowing (Sw), Emergency (Em), Floral Initiation (FI), Double rich appearing (DR), Terminal spikeled initiation (TS), Heading (Hd), Anthesis (At), Beginning of grain filling (BGF), Physiologic Maturity (PM), Harvest (Hv), and time of stem and spike growth with the dynamic of some of the yield components.

The average grain weight, variable from which bread and durum wheat present important differences (Zubaidi *et al.*, 1999; Reynolds *et al.*, 2004), seems for most crops related with grain number. Plants regulate grain number with its weight, in order that there is enough assimilates to fill the grains (Sadras, 2007, Ghiglione *et al.*, 2008; Gambín and Borrás, 2010). Some authors suggest that the relationship grain number *vs.* weight is under an important evolutionary genetic control, largely reducing the possible range size for each species (Sadras, 2007), and because of that the differences between wheat species could be constitutive rather than reflecting a different source-sink balance. Grain weight is generated from few days before anthesis until maturity (Calderini *et al.*, 2001; Ugarte *et al.*, 2007); period highly susceptible to water stresses (Ercoli *et al.*, 2008), and to high temperatures (McCaig, 1997; Savin and Nicolas, 1996; Calderini *et al.*, 1999b); thought, the grains potential size is largely determined between the end of the pre-anthesis phase and the beginning of the post-anthesis phase (Calderini *et al.*, 2001; Ugarte *et al.*, 2007). Furthermore, different grain sizes could be affected by high temperatures also differently, for bread wheat (Calderini *et al.*, 1999a) or for bread and durum wheat (Borghi *et al.*, 1995; Trethowan *et al.*, 2001).

The spike number m^{-2}, is the product from the sowing density and tillering (including tiller mortality) and is related with the coarser adaptation of grain number (Slafer *et al.*, 2014).

Despite that the main factor regulating tillering dynamics is the environment; there are large differences in tillering between the cereals and wheat species (Graham *et al.*, 1983; López-Castañeda and Richards, 1994), and due to its plasticity, the spikes per m^{-2} is critical for adaptation to resources availability (Satorre, 1999). A proper adjustment of tillering to the environment is related to a high efficiency in the use of radiation, water, in particular for dry conditions (Hadjichristodoulou, 1985), nitrogen and phosporus, since root production is related with the tiller number (Hockett, 1986). If tiller density is low the capture of resources will diminish, particularly radiation use in the early growth stages, and soil water evaporation will increase (Reynolds *et al.*, 2001), *e.g.* the uniculm cultivars commonly do not generate advantages in low-yielding conditions (Whan *et al.*, 1988). Differences between durum and bread wheat for that character can be found (Hurd, 1964; Zubaidi *et al.*, 1999) related to differences in water, nitrogen and phosphorous (Manske *et al.*, 2000) absorption at the early stages of growth (Liao *et al.*, 2004). Contrastingly, an excessive tillering can produce a deficient partition of resources to grains, in general the modern cultivars present a lower tillering, to avoid that many stems degenerate without grain (Siddique *et al.*, 1989a), commonly because competition around anthesis. In addition, the low tillering cultivars with low interplant competition should present advantages in high yield potential environments (Donald, 1968; Reynolds *et al.*, 1994).

The number of grains per spike is determined along the reproductive phase, with the initiation of floral primordia firstly and their survival to form grains later. In general, breeding has increased the number of grains per spike and per unit land area at the same time, through diminishing the competition between the growing spikes and stems during the stem elongation phase, known as 'critical phase' for grain yield generation (Slafer *et al.*, 2015) commonly because the introgression of dwarfing genes (Kirby, 1988; Siddique *et al.*, 1989b; Slafer and Whitechurch, 2001; Royo *et al.*, 2007).

In addition to yield components, other variables related to increases of biomass and stress adaptation could explain differences between the wheat species. In relation to increments in biomass, differences in the photosynthetic rate were found between cultivars of bread and durum wheat, suggesting that Chromosome D could be involved in depressing photosynthesis, by comparison between amphiploids (Austin *et al.*, 1982; Kaminsky *et al.*, 1990). Also the maintenance of photosynthesis performance in drought conditions seemed higher in durum than in bread wheat (Dias *et al.*, 2011). Nonetheless other works found similar photosynthetic capacity between bread and durum wheat (Fisher *et al.*, 1981; Rees *et al.*, 1994). Additionally, differences between the species for leaf angle (Acevedo, 1992), chlorophyll content and flag leaf area (Rees *et al.*, 1994) have been found. Related to stress adaptation, through a faster crop establishment, durum wheat presented longer coleoptiles which could favour crop establishment (Trethowan *et al.*, 2001). Regarding the water economy, differences may exist in water use (WU) (Blum, 2005); *e.g.* longer roots –which can allow mobilizing water from deeper soil layers- were reported for durum wheat (Wang *et al*., 2007); in addition to differences in water use efficiency (WUE) (Zhang and Oweis, 1999), the relationship between yield and water use, related to a low Δ^{13}C. Genetic variation for transpiration rates, affecting canopy temperature and the isotopic discrimination of Δ^{13}C were found for bread (Farquhar and Richards, 1984; Fischer *et al*., 1998; Sayre, 1996), for durum wheat (Giunta *et al*., 2008), and for both species of wheat (Monneveux *et al*., 2004; Misra *et al*., 2006). Nonetheless, there is dispute in the literature on the realistic value of increasing WUE and the basis of the dispute is that WUE and WU may not be totally independent traits (and then improving for WUE might result in cultivars less able to capture water). For instance, when water is not limiting or rains are highly irregular a high *WUE* or a low Δ^{13}C (Araus *et al*., 1998; Merah, 2001, Blum, 2009) can result in a reduced amount of water use, that can be incompatible with the good yields in most of environments (Blum, 2005, 2009).

Some of the difficulties to find general assumptions in the relative performance of both species are the complexity of the factors involved in yield formation, the limited number of variables which can be determined in each experiment, and the difficulty to accommodate a large degree of variability within particular experiments. In fact, most of the experimental assays comparing bread and durum wheat in the same environmental conditions were carried out under a very limited range of environments, many times limited to yield potential conditions (*e.g*. Fischer and Maurer, 1978; Aggarwal *et al*., 1986; Acevedo, 1991; Josephides, 1992; López-Castañeda and Richards, 1994; Palumbo and Boggini, 1994; Zubaidi *et al*., 1999; Calderini *et al*., 2006) and unfortunately, little is known based on solid experimental bases about the possible differential adaptation (presumed by the consistent pattern of distribution of these crops with respect to the yielding conditions) of these species to the environment, and the expected G X E interactions, and even less from the causes producing them. Furthermore, the scattered results from these limited attempts commonly show opposite conclusions or are inconclusive and in general, a direct extrapolation of knowledge from one species to another, as is commonly done in the literature, prevents the understanding of their specific differences. For this reason it is highly relevant to understand the environmental adaptation of the major physiological determinants with the aim of developing new selection criteria for breeding and to use the genotypes more efficient or productive for a given environment and ultimately rationalize land use to increase field crops productivity. Therefore, it would be important to test scientifically the assumptions derived from the pattern of land allocation suggesting that bread wheat would be higher yielding than durum wheat under relatively aleviated stress conditions and vice-versa.

5. Objectives

The overall aim of this thesis was to compare the bases of the differences in productivity between bread and durum wheat under a wide range of environmental conditions, particularly with important variations in water and N availability in contrasting growing seasons. The working hypothesis, based on the most common pattern of land allocation between these two species, is that durum wheat would possess attributes making it more tolerant or adapted to stressful conditions whilst bread wheat would possess attributes conferring higher yield potential.

To address the overall aim, I pursued the following specific objectives:

I. To quantify the differences in performance, in productive terms, between bread and durum wheat in a wide range of environmental conditions (Chapter II).

II. To identify differences in the species yield components and biomass growth, partition and dynamics along the environments (Chapter III).

III. To study the origin of the possible species differences in performance by analyzing yield and biomass formation and partition before and after anthesis (Chapter IV).

IV. To identify differences in the species morphology (leaves, tillers, roots) and growth dynamics in relationship with the adaptation to the variations of the environments (Chapter V).

V. To analyze the uptake and use efficiency of resources, in particular for the radiation, water and N, under the studied wide range of experimental conditions (Chapter VI).

The main approach used to achieve the aims was to run a set of field experiments in which both types of wheat were grown side-by-side throughout three consecutive growing seasons under contrasting water x N conditions in each case. Furthermore, I did review the literature, collecting data fragmentary available and meta-analysing these dispersed data in a single framework. In addition, as a subordinate objective I analyzed as a by-product the possibility of realizing good assessments of yield in earlier plant developmental moments by using the normalized difference vegetation index (NDVI), overall a group of bread and durum cultivars and water and N treatments and included this analysis as an Annex to the thesis.

6. Outline of the thesis

The present thesis is constituted by seven chapters and an annex. It includes this general introduction (Chapter I), six experimental research chapters (Chapters II, III, IV, V, VI), a general discussion with conclusions of the whole work (Chapter VII), and an annex reporting on the relationships between yield and NDVI measurements taken in pre-anthesis. In addition to unpublished results, this thesis includes data from two research papers published in SCI journals (Marti *et al.*, 2007; Marti and Slafer, 2014). However, for convenience with the traditional structure of a thesis, results have been divided into chapters following the different relevant issues of study (and not respecting the information gathered in the papers). As each chapter intends to be independently understood, all the chapters include the common regular sections of a scientific paper, but I tried to avoid repetitions, particularly with the materials and methods and in the introductions, leaving very concise introductions for each experimental chapter.

Chapter II includes experimental evidences to contrast the species relative performance in yield, comparing our experimental data with most of the existing literature data; Chapter III presents experimental evidences of the yield components generating yield differences, considering both numeric components and growth components; in Chapter IV I studied in further detail the generation of differences in yield and biomass mainly as a consequence of differences in sink-strength; Chapter V presents a descriptive research of some morphological differences between wheat species; and Chapter VI shows experimental evidences of capture and use of resources. Chapter VII offers a brief general discussion and conclusions. Finally, Annex I contains an analysis of the possibility to assess yield from indirect measurements done in early stages of development.

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Chapter II: Bread and durum wheat yield interaction with the environment under a wide range of environmental conditions

Abstract

It is frequently assumed that durum wheat is more tolerant to stress than bread wheat. Unfortunately few research papers compare the performance of both species side-by-side under a wide range of environments in field conditions. I aimed to compare durum and bread wheat performance in a field study under contrasting treatments of water and nitrogen during three experimental seasons. In addition I compiled a comprehensive database with data from field experiments in which both species were grown in the same field conditions. A cross-over interaction of yield from bread vs. durum wheat was found, but oppositely to the hypothesis, bread outyielded durum wheat in the low-yielding conditions while durum wheat tended to have higher yield potential. Further dividing the database in decades in which the cultivars were released, it was found that in the 1960s bread wheat outyielded durum wheat in almost any comparison, whilst contrastingly in the 2000s durum wheat outyielded bread wheat, on average for the database, in most of the environments; further confirming that the new durum CIMMYT cultivars had overtaken bread wheat under high-yielding environments, and suggesting that the differences in breeding may be under the association of durum wheat cultivars with lower yield potential.

Keywords: Triticum, yield, yield stability, breeding.

1. Introduction

In the Mediterranean basin; where both bread and durum wheat are sown, it has been traditional to grow durum wheat under relatively lower-yielding conditions in comparison to bread wheat, commonly sown under higher-yielding conditions, as explained in detail in Chapter I.

However, in addition to the uncertainty given by the scarcity of studies, the results available in the literature are not commonly consistent. While some studies do support the assumption that durum wheat is more drought-tolerant and would yield more in low-yielding conditions than bread wheat (López-Castañeda and Richards, 1994; Trethowan *et al*., 2001) others found opposite results (Josephides, 1993; Palumbo and Boggini, 1994; Zubaidi *et al*., 1999). The inconsistency may be due to the lack of a wide range of experimental environments in each of the studies, or because cultivars used for both species would have not been selected with the same criterion (*e.g.* in terms of yield potential). It might also be the case that breeding of these two species had not progressed simultaneously and the relative behaviour might have changed with time along the last decades. For instance, it seems that new durum cultivars derived from lines produced by CIMMYT would have overtaken bread wheat yield in high-yielding environments (Pfeiffer *et al*., 2001; K. Ammar, CIMMYT, personal communication, 2011). Unfortunately there is no experimental evidence supporting whether this is an exceptional behaviour of recently released cultivars of durum wheat from CIMMYT or a more generalised situation with durum wheat breeding globally.

To attempt resolving the uncertainties derived from the scarce number of comparative analyses, fragmentarily available in the literature and generally considering a limited range of environments in each particular study, I (i) run a set of field experiments with well adapted bread and durum wheat cultivars exploring a very wide range of environments in a Mediterranean agricultural region, and (ii) searched in depth the literature to identify papers reporting on performance of both wheat species were grown together under field conditions, and analysed all collected data together to draw general conclusions on the likely species-by-environment interaction that would be behind the pattern of land allocation to them. Therefore, based (i) on the consistent pattern of distribution of these crops with respect to the yielding conditions, particularly in the Mediterranean basin, and (ii) on references made in the literature, regarding durum wheat being more stress-adapted, I hypothesised that durum wheat would outyield bread wheat under low-yielding conditions though under stress free conditions bread wheat would outyield durum wheat.

2. Materials and methods

2.1 Field experiments

Three field experiments were carried out within a region of rainfed cereal production systems, in the Mediterranean location of Agramunt, province of Lleida (Catalonia, North-Eastern Spain; lat. 41º 47′17′′ N, long. 1º 5′59′′ E, altitude 337 m). In all cases the experiments were installed in actual farmers fields, with a soil classified as Fluvisol calcari (FAO, 1990). In these experiments I directly compared the performance of both bread and durum wheat under a wide range of environmental conditions given by the combination of different growing seasons (2004-05, exp. I; 2005-06, exp. II; 2006-07, exp. III) and water x nitrogen treatments (these treatments were imposed to create drastic differences, not to determine curves of responsiveness to these factors) in each of the seasons.

Sowing date was always in November (Table 1) within the optimal period for sowing cereals in the region and plant density was also within the ranges normally recommended (200-250 plants m^{-2}; Table 1). Weeds and diseases were controlled using agrochemicals following the manufacturer's recommendations for application. In all the experiments, soon after seedling emergence, plots were inspected and several segments of 50 cm on central rows having the exact targeted density, uniformly distributed, were labelled for sampling later in the season.

The first experiment consisted of the factorial combination of six genotypes (three bread and three durum wheat cultivars), two levels of water availability and two levels of N availability (Table 1). The three cultivars of each species (similar in growth cycle) were well adapted to the region, based on comparative yield trials of previous years published in reports of the GENVCE network (Group for the Evaluation of New Varieties of Field Crops). The two contrasting levels of water availability were rainfed throughout the growing season and irrigated from early spring (roughly coinciding with jointing) onwards on a weekly basis. The two contrasting levels of N availability were unfertilized and heavily fertilized with ammonium nitrate at a rate of 200 kgN ha^{-1} 49 days after sowing (before the onset of active growth at the end of winter). Treatments were arranged in a split-split-block design with three replications: the main plots were the combination of genotypes and irrigation levels, while the sub-plots (16 rows, 18 cm apart and 4 m long) were N levels.

The other two experiments (Exps. 2 and 3) consisted on the factorial combination of two of the cultivars from exp. I, the same two levels of N availability used in exp. 1, and four levels of irrigation (Table 1), arranged in a split-split-plot design with three replicates, the combination of genotypes and irrigation treatments were assigned to main plots with experimental units (sub-sub-plots) allocated to N treatments, of 17 rows, 18 cm apart and 5 m long.

Table 1
General conditions and treatments imposed in each of the three field experiments carried out in Agramunt (Catalonia, Spain).

Exp.	**General Conditions**				**Treatments**				
	Sowing date and density	**Initial soil content***		**Rainfall** (mm)	**Irrigation**		**Fertilization** (kg N ha^{-1})	**Genotype**	**Year of release**
		Mineral N (kg N ha^{-1})	**Available Water*** (mm)		**Treatment**	**Amount** (mm)			
I	16-Nov-04 250 plants m^{-2}	67	108	163	Rainfed	0	Unfertilized	Anza (Bread) Claudio (Durum) Provinciale (Bread) Simeto (Durum) Soissons (Bread) Vitron (Durum)	1974 1998 2001 2002 1990 1983
					Irrigated (from jointing to harvest)	165	Fertilized (200 kg N ha^{-1})		
II	28-Nov-05 200 plants m^{-2}	97	214	95	Rainfed	0	Unfertilized	Provinciale (Bread) Claudio (Durum)	2001 1998
					Irrigated (from jointing to harvest)	162			
					Irrigated (from jointing to anthesis)	107	Fertilized (200 kg N ha^{-1})		
					Irrigated (from anthesis to harvest)	55			
III	6-Nov-06 200 plants m^{-2}	87	162	326	Rainfed	0	Unfertilized	Provinciale (Bread) Claudio (Durum)	2001 1998
					Irrigated (from jointing to harvest)	316			
					Irrigated (from jointing to anthesis)	228	Fertilized (200 kg N ha^{-1})		
					Irrigated (from anthesis to harvest)	88			

*to 1 meter deep; available water is total water content minus the percentage that is under the permanent wilting point for each soil.

The two cultivars (Claudio and Provinciale) were selected on the basis of their performance across water x N conditions in the first experiment. The irrigation treatments included the extreme cases of the previous experiment (rainfed throughout and well irrigated from jointing onwards) plus two treatments in which irrigation was only applied either before or after anthesis (Table 1).

From anthesis to maturity each experimental unit was sampled weekly (each sample of 50 cm of a central row labelled earlier) for grain weight. They were oven-dried for 3 d at 60 ºC and weighed. The sample taken at maturity was twice the size of the previous samples (two 50 cm of central rows previously labelled) and the raw data of variables measured weekly were adjusted for each experimental unit by non-linear regression to a logistic curve against accumulated thermal time (Tb = 0 ºC), with the NLIN procedure from SAS software (SAS Institute, 2004), all relationships where highly significant ($R^2 > 0.90$; $P < 0.001$) and yield was determined.

2.2 Literature data

To search for papers to be included in the analysis, I used the Web of Science database. I searched the database on 20/10/2012, without time limits, with the key words 'wheat' AND 'bread' AND 'durum'. From the output of the search I looked individually for the papers in which experiments included both bread and durum wheat grown simultaneously under field conditions. Then, from the few papers meeting the selection criteria, I further expanded the database by including additional papers meeting the criteria which not being in the output of the search had been quoted by those retrieved from the search. The resulting database had 64 papers reporting collectively on 470 different cultivars of bread and durum wheat in a wide range of conditions (Table 2), exploring yields from virtually zero to almost 9 Mg ha^{-1}. Although more than 20 papers were published after 2003 (and 15 between 2006 and 2010) there were only 2 papers which cultivars of both wheat species grown in the experiments had been released after 2000. Therefore, apart from data taken from published papers reporting experiments with both wheat species grown together, I further expanded the database, to include cultivars released in the last decade (2000-2010), and elite advanced lines, from CIMMYT, comparing data from the Elite Durum Yield Trial and the Elite Spring Wheat Yield Trial; and from the International Durum Wheat Yield Nursery and the International Bread Wheat Screening Nursery (available in http://apps.cimmyt.org). These trials were separate for durum and bread wheat, but they were sown in the same location under similar experimental conditions. When conditions were not similar (for instance if in a particular location the management given to bread and durum wheat was not the same), the data were disregarded.

2.3 Data analysis

Data from bread and durum wheat were analyzed using regression analyses. In all the analyses when regressing a variable in bread wheat against the same variable in durum wheat both variables were subjected to error, thus I fitted the regressions with Model II (Ludbrook, 2012).

Table 2. Description of the numbers of environments and cultivars of durum and bread wheat included in each paper as well as the range of years of release of these cultivars.

Exp. location	**Number of environments**	**Number of cultivars**		**Years of release**	**References**	
		Durum	**Bread**			
Goondiwindi, Roma; *Australia*	3	1	1	1988-1998	Dang *et al.* (2006)	
Walgett, Tamworth; *Australia*	27	1	2	1986-2000	Kirkegaard *et al.* (2004)	✓
Condobolin, Moombooldool; *Australia*	4	2	4	1984-1987	López-Castañeda, Richards (1994)	✓
Narembeen; *Australia*	2	2	1	1985-1998	Miyan and Anderson (2003)	
Roseworthy, Palmer; *Australia*	6	14	4	Landrace-1993	Zubaidi *et al.* (1999)	✓
Swift Current; *Canada*	3	2	2	1968-1990	Cutforth *et al.* (1988) Clarke *et al.* (1990)	
Indian Head, Lemberg, Yorkton; *Canada*	5	1	3	1990-1991	Gan *et al.* (2000)	✓
Lethbridge; *Canada*	8	1	7	1969-1990	Major *et al.* (1992)	✓
Swift Current; *Canada*	2	5	6	1907-1998	Wang *et al.* (2007)	✓
Undefined; Cyprus	115	3	3	1962-1983	Josephides (1993)	
Akaki, Robe; *Ethiophia*	4	1	1	1981-1982	Geleto *et al.* (1996)	✓
Addis Ababa, Debre Zeit, Inewari; *Ethiopia*	24	3	5	1974-1992	Shulthess *et al.* (1997)	✓
Thessalonica; *Greece*	5	3	2	1945-1971	Papakosta and Gagianas (1991)	✓
Indore; *India*	4	5	15	1979-1999	Behera *et al.* (2007)	✓
Pune; *India*	3	14	16	-	Misra *et al.* (2006)	
New Delhi; *India*	10	6	6	1969-1976	Sinha *et al.* (1986) Aggarwal *et al.* (1986 a,b)	✓
Khorasan-e-Razavi; *Iran*	4	4	1	1995-1997	Moayedi *et al.* (2010)	✓
Milano, Viterbo, Catania; *Italy*	12	4	4	1974-1998	Borghi *et al.* (1995)	✓
8 locations; *Italy*	11	23	21	-	Gavuzzi *et al.* (1993)	
Libertinia; *Italy*	3	4	4	1950-1986	Palumbo and Boggini (1994)	✓
Jubeiha; *Jordan*	4	3	1	1960-1976	Duwayri (1984)	✓
Ciudad Obregon, Texcoco; *Mexico*	2	2	2	1988-1992	Calderini *et al.* (2006)	✓
Ciudad Obregon; *Mexico*	12	9	46	1954-1975	Fischer and Maurer (1978)	✓
Ciudad Obregon; *Mexico*	4	8	33	1964-1973	Fischer and HilleRisLambers (1978)	✓
Ciudad Obregon; *Mexico*	1	5	11	-	Monneveux *et al.* (2003)	
Ciudad Obregon; *Mexico*	1	20	20	-	Monneveux *et al.* (2004)	
Ciudad Obregon; *Mexico*	10	8	14	1962-2001	Nalley and Barkley (2007)	✓
Ciudad Obregon; *Mexico*	4	5	6	1984-2000	Ortiz-Monasterio *et al.* (2002)	✓
Ciudad Obregon; *Mexico*	6	7	7	1962-1989	Reynolds *et al.* (2002)	✓
Ciudad Obregon; *Mexico*	24	6	10	-	Singh *et al.* (2001)	
Ciudad Obregon; *Mexico*	8	3	9	1945-1971	Sojka *et al.* (1981)	✓
Riyadh; *Saudi Arabia*	2	3	2	1970-1977	Sayed and Ghandorah (1984)	✓
Jerez de la Frontera; *Spain*	2	5	5	1970-2003	Cátedra and Solís (2003)	
Lleida; *Spain*	14	1	1	1988-1998	Cossani *et al.* (2009) Cossani *et al.* (2012)	✓
Cordoba; *Spain*	2	1	1	1975-1984	Gallardo and Fereres (1993)	
Carrasco, Dehesilla, Saladilla, Sta. Clara; *Spain*	48	1	1	1990-1992	López-Bellido *et al.* (2008)	✓
Lleida; *Spain*	4	3	3	1975-2000	Marti *et al.* (2007)	✓
Breda, Tel Hadya; *Syria*	18	4	4	1969-1977	Anderson (1985a,b)	✓
Tel Hadya; *Syria*	12	1	1	1989	Karrou and Oweis (2012)	
Tel Hadya; *Syria*	8	4	4	1965-1993	Oweis *et al.* (1998) Oweis *et al.* (1999) Oweis and Hachum (2003)	
Tel Hadya; *Syria*	38	5	4	1989	Zhang and Oweis (1999)	✓
Konya; *Turkey*	8	4	16	Landrace-1997	Bagci *et al.* (2007)	✓
Izmir; *Turkey*	1	10	5	1970-1995	Budak (2001)	
Konya; *Turkey*	2	2	2	1967-1999	Cakmak *et al.* (1997)	✓
Konya; *Turkey*	4	2	2	1967-1979	Ekiz *et al.* (1998)	✓
Ankara, Eskisehir, Konya; *Turkey*	16	1	1	1967-1979	Halitligil *et al.* (2000)	
Ankara; *Turkey*	5	1	1	1968-1991	Inal *et al.* (2003)	
Eskisehir, Konya; *Turkey*	2	1	7	1966-1995	Kalayci *et al.* (1998)	✓
Eskisehir; *Turkey*	4	3	37	1936-2002	Kalayci *et al.* (1999)	✓
Tulelake; *USA*	4	2	2	1966-1976	Baghott and Puri (1979)	
Davis, El Centro, Tulelake, *USA*	12	3	6	1970-1994	Brevis and Dubcovsky (2010)	
Moreno Valley; *USA*	9	2	12	Landrace-1980	Dhugga and Waines (1989)	✓
Moreno Valley; *USA*	6	5	9	Landrace-1991	Ehdaie *et al.* (2001) Ehdaie and Waines (2001)	✓
Moreno Valley; *USA*	4	1	10	Landrace-1991	Ehdaie *et al.* (2008)	✓
Brawley; *USA*	13	2	1	1974-1979	Francois *et al.* (1986)	✓
Morris; *USA*	9	1	1	1978-2000	Jaradat (2009)	✓
Kansas; *USA*	2	1	1	1999-1994	Marque *et al.* (2004)	✓

✓Papers included in the analysis per decade of release because either the authors informed the year of release of the cultivars or we were able to identify the year of release of the cultivars used in specialised web sites (*e.g.* grain genes, http://wheat.pw.usda.gov; European wheat database, http://genbank.vurv.cz/ewdb/; wheat atlas, http://wheatatlas.cimmyt.org). Papers not included in this particular analysis either used cultivars which we were not able to identify their year of release or the two types of wheat were released in different decades.

3. Results

3.1 Environmental range and yield in NE Spain experiments

Our field experiments presented a wide variety of environmental conditions given by 3 experimental years (which varied greatly in water availability, as usual in Mediterranean regions) in combination with N and irrigation treatments that produced an important range of biomass (*c*. 2.3-19.6 Mg ha^{-1}) and yield (*c*. 0.6-8.7 Mg ha^{-1}).

The first cropping season had lower rains (163 mm) than the average for the zone (Nov.-June 273 ± 94 mm) which additionally arrived late, only half of the seasonal rain fell before flowering (Fig. 1, exp. 1), with relatively low amounts of water stored in the soil before sowing (Table 1) and irrigation only started at the onset of stem elongation. In this condition yields were very low (Fig. 2) particularly so in the rainfed conditions (0.9 Mg ha^{-1} averaging across cultivars, and 1.16 Mg ha^{-1} for the best performing cultivars, Claudio and Provinciale), though even in the irrigated treatment yields were rather low (*c*. 3 Mg ha^{-1}) and the weekly irrigation, from jointing to harvest, produced *c*. 1.7 Mg ha^{-1} more than the not irrigated (*c*.1 Mg ha^{-1}) while the effects of the N treatment were little producing *c*. 0.3 Mg ha^{-1} more in average for all conditions than the unfertilized (*c*. 1.7 Mg ha^{-1}). In this low-yielding conditions bread wheat tended to yield more than durum wheat (Fig. 2, exp. 1).

The second experimental season was intermediate, despite the little rains (95 mm), started with a large amount of water stored in the soil (214 mm) and additionally rainfall came almost entirely before flowering (Fig. 1, exp. 2), producing medium yields for the zone (rainfed treatments yielded an average of *c*. 4 Mg ha^{-1}). Weekly water treatments, as typically applied in the zone during the more active period of growth (from jointing to maturity) generated *c*. 2.3 Mg ha^{-1} more than the rainfed treatment 4.1 Mg ha^{-1}. Due to the high initial levels of N contained in the soil (97 kg ha^{-1}) in addition to the moderate rains that year the nitrogen treatment barely increased yield, and was not significantly different ($\alpha > 0.05$) from the unfertilized treatments. In this conditions both types of wheat tended to have similar yields (Fig. 2, exp. 2).

The third growing season was high-yielding for the zone, as rainfed plots yielded *c*. 6 Mg ha^{-1}, because of the high amount of water stored in the soil at the beginning of the season and the rather high rainfall during the wheat growing period 488 mm in total compared to the mean seasonal rainfall of the location (for the period 1975-2007 the average rainfall between November and June was 273±94 mm). Water treatments in those conditions, despite slightly increasing yield were not significantly different from the rainfed ($\alpha > 0.05$), the fully irrigated treatment yielded only *c*. 0.8 Mg ha^{-1} more than the rainfed *c*. 6 Mg ha^{-1}, and contrastingly N treatments were highly significant ($\alpha < 0.0001$) and achieved *c*. 2.6 Mg ha^{-1} more than the unfertilized 4.9 Mg ha^{-1}. In this high-yielding environment durum wheat tended to outyield bread wheat (Fig. 2, exp. 3).

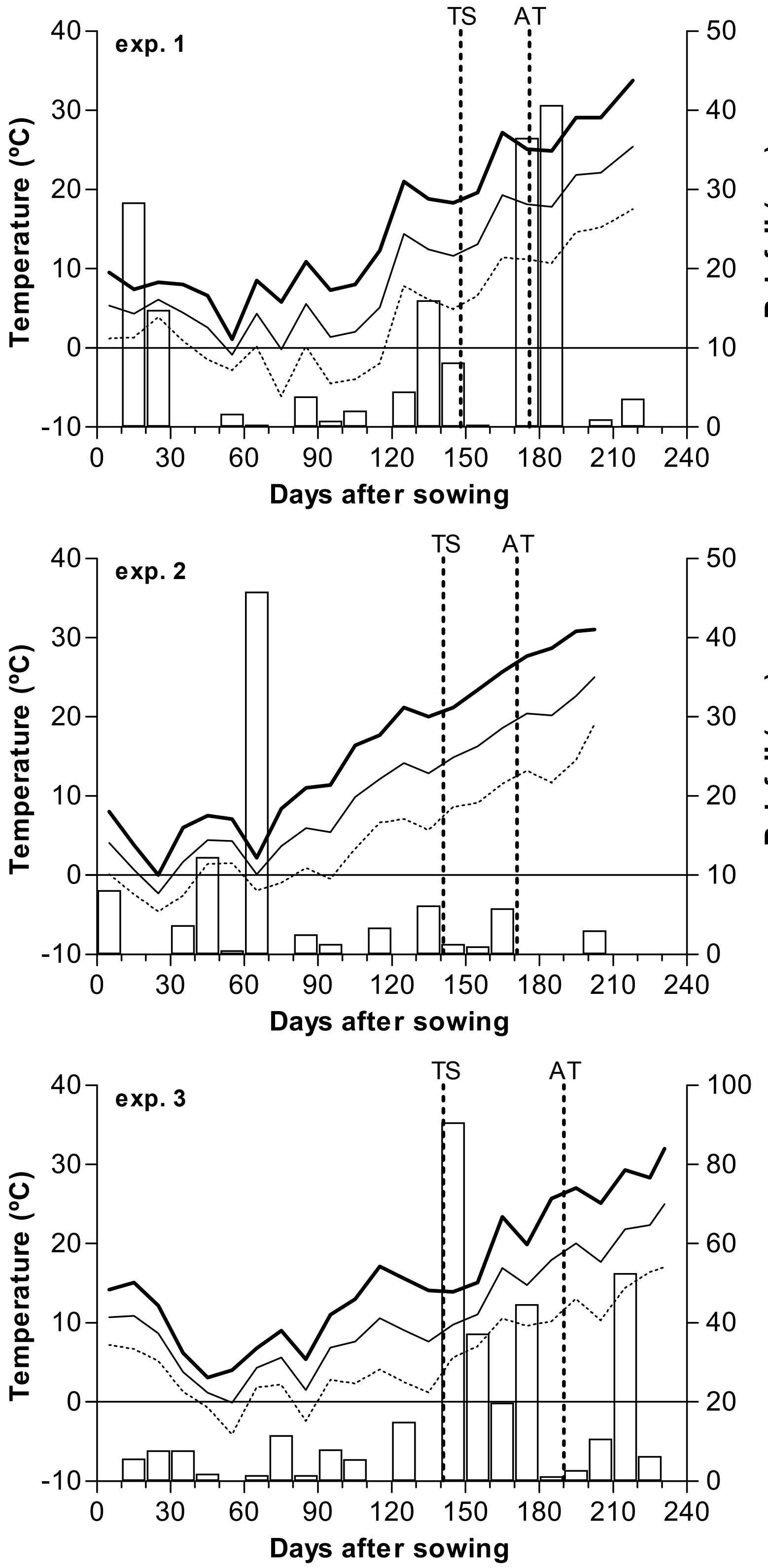

Figure 1. Meteorological conditions during the crop cycle in Lleida for the 3 experimental years. Values are 10 day means of medium (plain line), maximum (thick line) and minimum (dotted line) temperature, and 10 day accumulated precipitation (columns). Dashed vertical lines indicate the dates of terminal spikeled initiation (TS) and anthesis (AT).

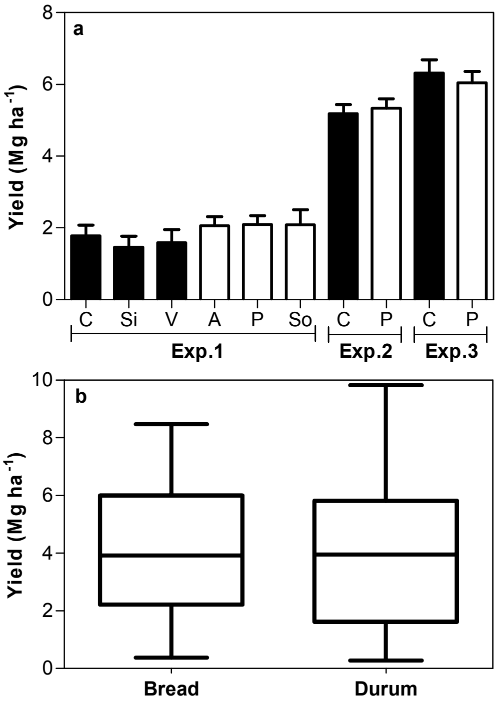

Figure 2. Yield of durum wheat (closed bars) and bread wheat (open bars) grown side by side through a wide range of conditions in each of the three experiments carried out at Agramunt, NE Spain (a); and boxplot of bread and durum wheat yield across all growing conditions of these experiments (b). In panel (a) the initials stand for the cultivars Claudio (C), Simeto (Si), Vitron (V), Anza (A), Provinciale (P), Soissons (So).

Therefore, despite that the means from both species along our experimental conditions where similar (*c.* 4 Mg ha^{-1}; Fig. 2b), the standard deviation was larger for durum than for bread wheat (2.51 *vs.* 2.21 Mg ha^{-1}), and therefore yield of durum wheat had a higher potential in stress-free conditions, but was more severely penalised in the lowest-yielding environments, than bread wheat across the experiments carried out in NE Spain (Fig. 2b).

3.2 Overall differences in yield between bread and durum wheat

The data from the experiments carried out in NE Spain and the dataset from published results fell in the same cloud of data-points (Fig. 3), indicating that our results may well represent what is a general situation for relative performance of durum and bread wheat, beyond the location and cultivars used.

Expectedly, there was a strong positive relationship between yields of durum and bread wheat along the very wide range of environmental conditions explored (Fig. 3), as both cereals respond broadly similarly to changes in environmental conditions. However, a closer inspection of the data reveals that for both the data of the experiments carried out in NE Spain and those taken from the literature (i) the coefficients of regression were significantly lower than 1, and not substantially different between them (0.86±0.03 for our experiments;

0.91±0.01 for the literature data); and (ii) the intercepts were higher than zero (0.69±0.19 and 0.46±0.03 Mg ha^{-1}; for the data from our experiments and from the literature, respectively). This means that not only in our experiments, but also in the joint analysis of fragmented data dispersed in the literature, bread wheat consistently outyielded durum wheat in severely stressed environments while durum wheat possessed a higher yield potential (Fig. 3).

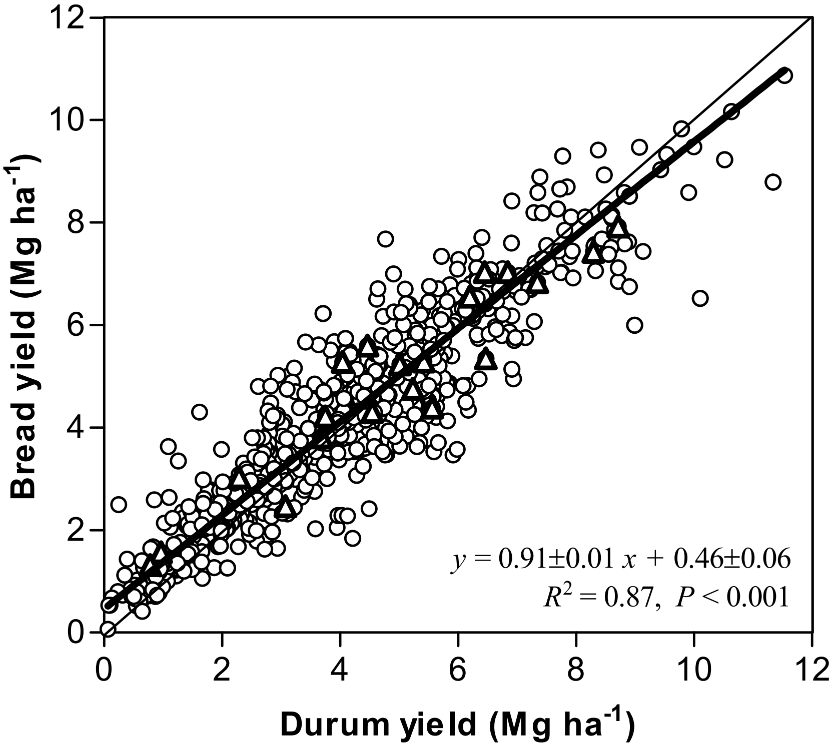

Figure 3. Relationship between bread and durum wheat yields with data collected from published studies (Table 2; circles) and from the different experiments carried out in NE Spain (Table 1; triangles). The thick line and the equation stand for the regression analysis of all data together (the parameters of the regressions for the data from our experiments and from the literature fitted separately did not differ significantly; $P > 0.1$). The thin line stands for the 1:1 ratio.

3.3 Did breeding affect the relationships of durum and bread wheat yield?

As the pattern of durum wheat having consistently more yield potential than bread wheat, and the latter performing consistently better under severe stress than the former was unexpected (the opposite of what I hypothesised, based on the pattern of land use and assertions made in several references in the literature), I wanted to establish whether the overall trends found in the present study was altered by breeding during the last decades. To test whether this situation was a consequence of a differential progress achieved by breeding of both species since the green revolution, I categorised the database by the decade of release of the cultivars that were used in the different studies reviewed (Table 2).

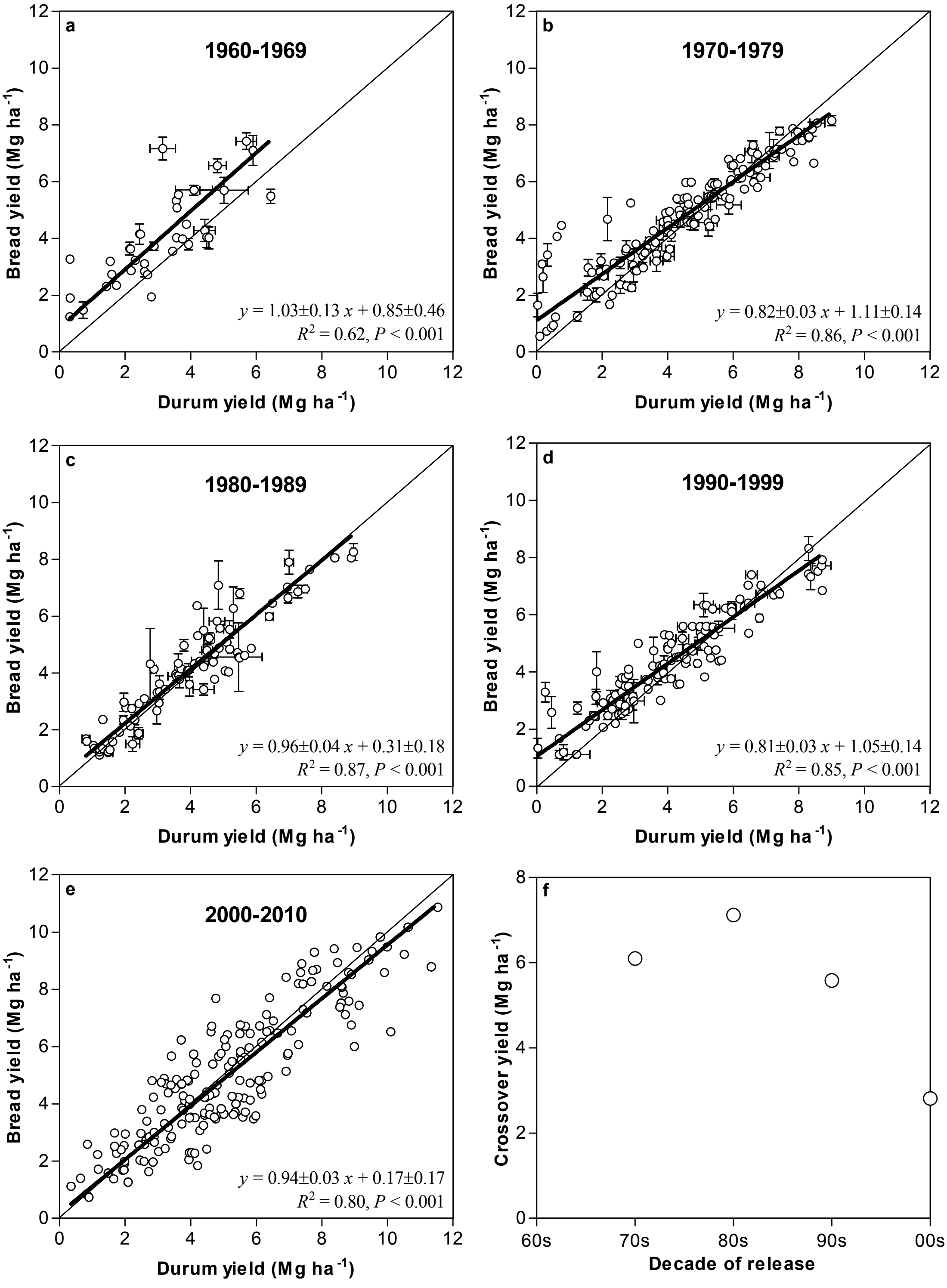

Figure 4. Relationship (i) between bread and durum wheat yields from Fig. 3 divided upon decade of release of the cultivars (1960s (a); 1970s (b); 1980s (c); 1990s (d); and 2000s (e)); and (ii) between yield level at which the regression lines crossed-over the 1:1 line and the decade of release of the cultivars (f). Segments show standard deviation of the means when data points are averages of more than 1 cultivar (a-d), whenever the magnitude of the SD was larger than the size of the symbol. The light lines stand for the 1:1 ratio (a-e); and the thick lines and the equations stand for the regression analyses. In the last panel there is no data-point for the 1960s because the regression did not crossed-over the 1:1 line in that decade.

Focusing on cultivars of both species released in the 1960's, the relationship was weaker than that for the overall dataset and, more importantly, the cases in which durum wheat yielded more than bread wheat were exceptional in number and negligible in magnitude of yield difference (Fig. 4a). In fact, the line fitting the relationship between bread and durum wheat yields never crossed-over the 1:1 ratio (Fig. 4a), bread wheat in that decade would expectedly yield more than durum wheat at any yielding condition.

On the other extreme, considering cultivars released in the last decade (and advanced elite lines of CIMMYT) durum wheat outyielded bread wheat in more than half of the cases (54 %, Fig. 4e), and the regression line crossed-over the 1:1 ratio at *c*. 3 Mg ha^{-1} (Fig. 4e,f), a yield level easily achievable in this decade in many wheat growing regions.

The other three decades showed intermediate values of both the proportion of cases in which yield of durum was higher than that of bread wheat and the yield level of the crossover of the regression and the 1:1 lines (Fig. 4f). Consequently, there was a significant trend to consistently reduce the yield level of the cross-over the 1:1 line of relationship between bread and durum wheat yield in the last decades (Fig. 4f).

To illustrate these changes over time further I divided the database used for each of the five decades into three levels of yield (*i.e.* from 0 to 1/3 of maximum yield of that decade, from 1/3 to 2/3, and from 2/3 to the maximum yield achieved, and considered them representative of low-, medium- and high-yielding conditions in each case). Then for each yield condition I calculated the residuals to the 1:1 ratio in each panel of Fig. 4a-e and averaged them (*i.e.* the average difference in yield between bread and durum wheat for that yielding condition in each of the five decades analysed). In all yielding conditions a clear negative trend was presented (Fig. 5) implying that disregarding the yielding condition, durum wheat breeding seemed to have produced larger gains than bread wheat breeding. For the relatively low-yielding environments, bread wheat consistently yielded more than durum wheat, but the difference higher than 1 Mg ha^{-1} in the 1960's was reduced to less than 0.5 Mg ha^{-1} in the 2000's (Fig. 5a). For the medium-yielding environments bread wheat outyielded durum wheat in the 1960's but since then the average yields of both wheat species where rather similar (Fig. 5b). In the highest-yielding conditions the relative performance reversed and durum wheat outyielded bread wheat clearly, at least in the last two decades (Fig. 5c).

Overall, it seemed clear that the advantage of durum wheat in yield potential, exhibited consistently both in our experiments and in the meta-analysis with the database from the literature, reflects the fact that yield potential has been increased more markedly in durum than in bread wheat during the last few decades (Fig. 5c). On the other extreme of the relationship, although it seemed clear that bread wheat outyielded durum wheat under severe stress in the five decades analysed, the magnitude of the yield advantage seemed to have been reduced through time (Fig. 5a), simultaneously with the larger increases in yield potential of durum wheat.

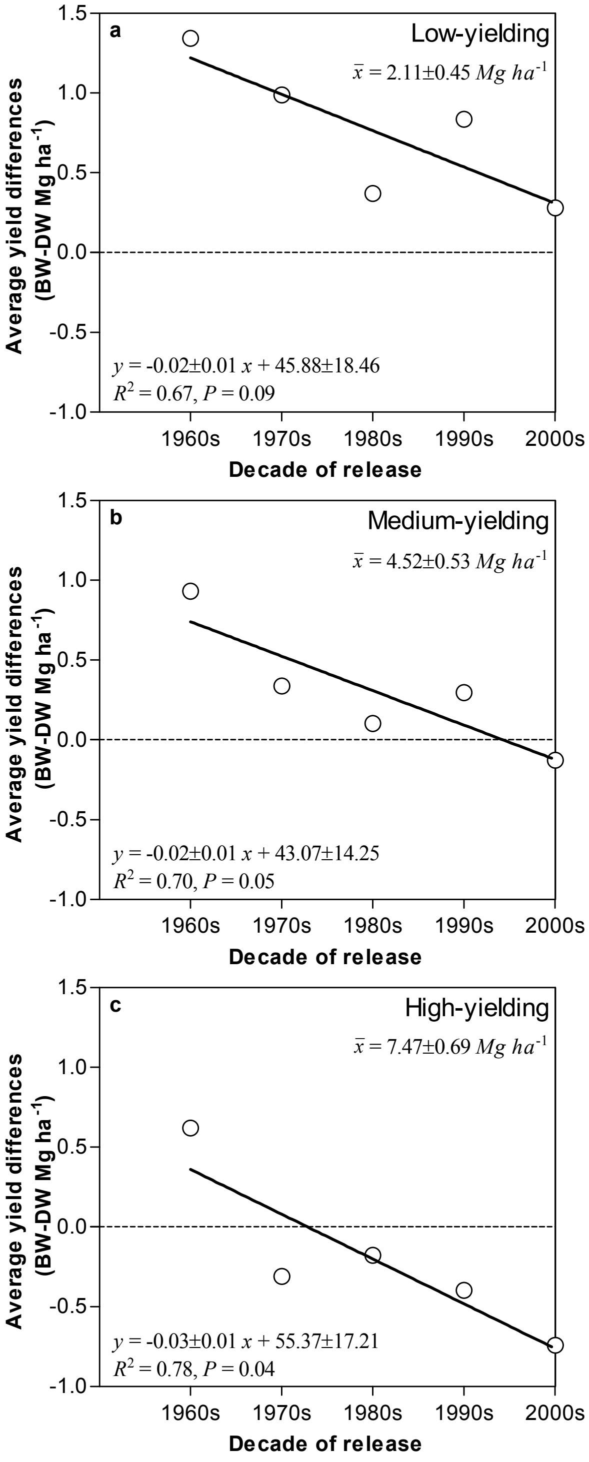

Figure 5. Average differences in yield between bread and durum wheat (positive values means bread wheat outyielded durum wheat in average and negative values the opposite). The plain thick lines and the equations stand for the regression analysis, and the dashed light line is the iso-yield (when durum and bread wheat had equal yields). Data were divided within each decade of release

into 3 yielding categories (low-, medium- and high-yielding conditions based on the range of yields explored in each case).

4. Discussion

The pattern in land use of growing durum wheat most commonly under lower-yielding conditions than bread wheat (*e.g.* Acevedo, 1991; Ceccarelli *et al*., 1987), noticeable in any statistical report (International Grains Council, 2010), likely based on the assumption that durum wheat deals better with Mediterranean stressful conditions than bread wheat (*e.g.* Monneveux *et al*., 2012), did not find support on the relative performance reported in the present paper. Species-by-environment interaction was found not only to be significant but also "cross-over" (*i.e.* the ranking of species varied with the environment). Oppositely to what I hypothesised, the outcome of the interaction was that bread wheat most frequently outyielded durum wheat in the low-yielding environments, whilst durum wheat clearly tended to have a higher yield potential than bread wheat. This trend was consistently found along the wide range of experimental conditions explored throughout N and water treatments in 3 growing seasons in a Mediterranean region as well as through the meta-analysis of the published data. This agreement from different sources strengthens the conclusions making them rather independent of particular cultivars of each species and of particular regions/seasons. Understanding the interaction found between both wheat species could be important to identify relevant traits for either stress tolerance or yield potential.

The belief that bread wheat might be higher-yielding than durum wheat (and therefore might posses a higher yield potential), likely the cause of the common pattern of land use mentioned above, could have been developed at the time of the green revolution. When the analysis of the data from the literature is restricted to cultivars that were released in the 1960's this was almost unequivocally the case. However, when the analysis involved cultivars more recently released, durum wheat outyielded bread wheat under high yielding conditions, and the yielding level at which this advantage became evident was systematically reduced during the last five decades. It seemed likely then, that bread wheat was subjected to higher breeding pressure (or its breeding process was more efficient) than durum wheat before and during the green revolution. But during the few decades elapsed from then on breeding for yield potential seems to have been more successful in durum than in bread wheat. This trend confirms what has been stated for the latest cultivars released by CIMMYT; *i.e.* durum wheat tended to consistently outyield bread cultivars in the highest yielding conditions (*e.g.* Pfeiffer *et al*., 2001). Then the relative performance seems to describe actually a more generalised pattern, not only apparent in CIMMYT material.

Explaining the causes behind the land pattern of durum most commonly sown under lower-yielding conditions is not straightforward. Likely durum wheat in its historical development in the near east could have accumulated a high number of stress-resistant traits (*e.g.* higher photosynthetic performance, in heat stress conditions, comparatively to either bread wheat; Dias *et al*., 2011, or *Aegilops* ssp. for cv. Cham-1; Rekika *et al*., 1997). In fact durum germoplasm carrying stress resistant genes were used in bread wheat breeding making for instance a significant contribution to the extension of the wheat belt into the drier areas of Australia (Marshall, 1987). However, only exceptional cases can be found in the analysis provided in the present study (from either the literature dataset or from our experimental data) of durum wheat having better yields than bread wheat under stressful conditions. Furthermore when analysing the few data comparing landraces of both durum and bread wheat in the same experiment (Karamanos *et al*., 2008), it can be found the same cross-over pattern with landraces of hexaploid wheat yielding better than those of tetraploid wheat under the lowest-yielding conditions. A possible explanation for the commonly reported pattern of land allocation could be founded in the belief that durum wheat have relatively low yield potential (as it was traditionally the case at the times of the green revolution) and that cultivars of lower yield potential can many times have a better performance under stress (*e.g*. Blum, 2005; Ceccarelli and Grando, 1991). In fact the trends depicted in the present study goes in the opposite direction: only when durum wheat yield potential was increased more substantially (in the last few decades) the yield difference with bread wheat under low-yielding conditions tended to be reduced. This is in line with the proposed idea that improving yield potential would concomitantly increase yield under stress (Calderini and Slafer 1999; Pedro *et al*., 2011; Slafer and Araus 2007; Tambussi *et al*., 2005).

Generally all the cross-over interactions (for the experimental and literature data) were significantly different from the 1 to 1 line; and then bread wheat might actually be a more reliable alternative than durum wheat for the rainfed Mediterranean systems and durum wheat to be an alternative to bread wheat in high yielding conditions, when fertilized adequately to achieve the requirements of protein concentration from the industry.

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Chapter III: Yield components

Abstract

Grain weight was constitutively higher in durum than in bread wheat, likely associated with a lower fruiting efficiency in the former; but in both types of wheat, grain number per unit land area, was the component responsible for yield sensitivity to environmental changes. In addition, grain weight stability was lower for durum but likely not as a consequence of a higher sensitivity to high temperatures but because of a lower capacity of regulation with grain number. Differences in yield were also related to differences in biomass and its partition, though when comparing the species relative performance along the environmental potential only the harvest index (HI) relative variation was significantly different from the 1 to 1 line, and likely the cross-over yield interaction found in chapter II, was more a consequence of differences in partition than in total accumulated biomass.

Keywords: Yield components, HI, Biomass, yield stability.

1. Introduction

As earlier discussed in Chapter II, the relative performance of the species, bread and durum wheat, presented a cross-over interaction with the yielding environment, in general for most of cultivars comparisons. A common approach to explain the variations and the generation of yield is made by dividing yield in its forming components, in an attempt to simplify the great complexity of that variable. However, two different approaches are commonly attempted, one by analysing the yield components "per se", (the number of grains m^{-2} and the individual grain weight) and the second by analysing the dry matter generation and partition to yield (Fig. 1).

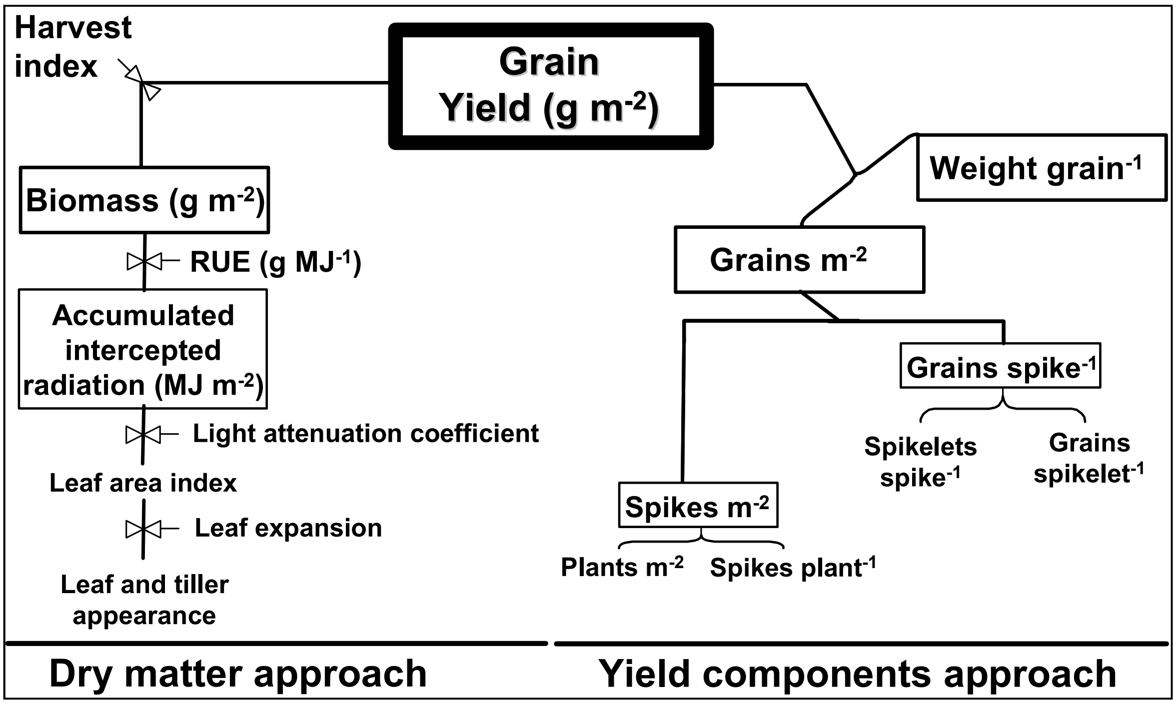

Figure 1. Representation of two different and complementary approaches for analyzing grain yield. The yield component approach (right panel) consists in dissecting grain yield into single numerical components. The dry mater approach (left panel) is based on dry matter accumulation (strongly dependent upon the ability of the crop canopy to intercept incoming radiation) and partitioning. RUE is radiation use efficiency. Adapted from Slafer and Savin (2006).

However, finding a clear explanation of the reasons behind the differences in yield performance in the literature is not straightforward given the relatively few studies in which the performance of both bread and durum wheat was directly compared in experiments growing them side-by-side, as explained in further detail in Chapter II; and in addition to the uncertainty given by the scarcity of studies, because the results available in the literature are not always consistent, perhaps as a consequence of the cross-over yield interaction. In the few comparisons available, regarding the biomass generation bread wheat was described to present a relatively earliness in biomass production (López-Castañeda and Richards, 1994; Zubaidi *et al.*, 1999) related to some early vigour and a higher number of tillers by m^{-2}, which favoured a rapid canopy establishment to eventually generate differences in interception of radiation and biomass, in particular for the dryer rainfed conditions (Zubaidi *et al*., 1999). While contrastingly, in other experiments the biomass at anthesis from both species was rather similar (Aggarwal *et al*.,1986) and durum wheat cultivars were found to present longer coleoptiles associated to early vigour in the emergence and heavier grains (Trethowan *et al*., 2001), and even in the experiments of López-Castañeda and Richards (1994) durums presented a shorter time to double ridge, being that overall the species and related with higher yields, despite both species presented similar times to anthesis.

Regarding the yield components attempt, while in general in most of the comparisons durum presented heavier grains and a lower number of them (*e.g*. Aggarwal *et al*.,1986; Josephides, 1993; Zubaidi *et al*., 1999; Trethowan *et al*., 2001; Reynolds *et al*., 2004); in contrast, Palumbo and Boggini, (1994) and Zubaidi *et al*., (1999) found them to be similar under drought prone conditions, and explained that as difficulties from durum to fill the grains when there was a post-anthesis drought. That was further supported by López-Castañeda and Richards, (1994) under drought conditions who found a post-anthesis lower growth rate of the relative culms and grains biomass for durum wheat, and by Aggarwal *et al*., (1986) who found durum more susceptible to changes in the post-anthesis biomass. Nonetheless, Reynolds *et al*., (2004) in a large comparison of cultivars and environments found durum more sensible to the pre-anthesis growing conditions, while little sensitive in comparison to breads to high temperatures around anthesis, and therefore high temperatures could play some role in determining the species differences in grain weight, furthermore Dias and Lidon (2009) found grain growth rate and potential grain weight related to higher yields under heat stress regardless of the species.

The inconsistency in the literature results may be a consequence of the lack of a wide range of experimental environments in each of the studies, or because cultivars used for comparing both species would have not been selected with the same criterion (*i.e.* in terms of yield potential). After the scarce number of comparative analyses, fragmentarily available in the literature and generally considering a limited range of environments in each particular study; to attempt improving the knowledge about the relative performance of the more commonly used wheat species, I further studied our set of field experiments and literature data, to draw general conclusions on the likely species-by-environment interaction that would be behind the yield components. The basic hypothesis is that the consistent species-by-environment interaction in yield is the consequence of few characters conferring an adaptive advantage to one particular species in a given environment and that will be possible to use that knowledge in breeding programs or in field management.

2. Materials and methods

2.1 Field experiments

From jointing to maturity each experimental unit, from the experimental setup explained in further detail in the materials and methods part from Chapter II, was sampled weekly (each sample of 50 cm of a central row labelled earlier). Samples were oven-dried for 3 d at 60 ºC and weighed for biomass. The sample taken at maturity was twice the size of the previous samples (two 50 cm of central rows previously labelled) and yield components were determined.

2.2 Literature data

The literature data was taken from those scientific papers, as reported in the Chapter II, which reported data about the yield components and biomass.

2.3 Data analysis

Data from bread and durum wheat were analyzed using regression analyses. In all the analyses when regressing a variable in bread wheat against the same variable in durum wheat both variables were subjected to error, thus I fitted the regressions with Model II (Ludbrook, 2012).

The raw data of biomass measured weekly was adjusted for each experimental unit by non-linear regression to a logistic curve against accumulated thermal time (Tb = 0 ºC) following the equation 1 (Darroch and Baker, 1990)

(eq. 1) $y = W[1 + \exp(B - Cx)]^{-1}$

Where y is the plot biomass and x the accumulated thermal time from sowing, W estimates the final biomass, B is related to both duration ad rate of growth, and C is related to rate of growth. Following their procedure the parameter maximum crop growth rate (MCGR), was calculated as MCGR = $CW\ 4^{-1}$, the total duration of crop growth (T), since the function never reach its asymptotic maximum W, T was calculated as the thermal time when $y = 0.95W$ and the active crop growth duration (ACGD) was calculated as the time from $y = 0.05W$ to $y = 0.95W$. The fits were calculated with the NLIN procedure from SAS software (SAS Institute, 1999), all relationships where highly significant ($R^2 > 0.90$; $P < 0.001$). From the total biomass fits was calculated the crop growth rate (CGR) as the average accumulated biomass from one sampling to the next one.

3. Results

3.1 Environmental variation in temperature for the 3 experimental years

Despite the average temperatures along the crop cycle where rather similar (9.7, 9.9 and 10.59 ºC, respectively for each season), during the stem elongation period (SE) the exp. 2 had the highest picks of temperature, up until 35ºC, coinciding with the moment of anthesis while in the exp. 1 and 3 the maximum temp during that period were 31ºC. Regarding the post-anthesis period the exp. 2 was slightly warmer than the others (21.3, 21.7 and 20.5ºC, respectively for each season); however, the highest picks of temperature were at the end of exp. 1 with 37ºC, contrastingly in the exp. 3 temperatures were well below 35ºC, the threshold above which grain growth is severely affected by heat shocks (Savin and Nicolas, 1996) and grain filling took place under relatively mild conditions.

3.2 Grain number and average grain weight in the whole dataset

The grain number was the main component related to yield upon the yielding range explored, considering the whole dataset ($R^2 = 0.82$ and $R^2 = 0.86$ for the literature, and $R^2 = 0.97$ and $R^2 = 0.94$ for our experiments, for bread and durum wheat respectively; $P < 0.001$). On the other hand, in none of the two species yield was significantly related to the average size of the grains (for the data taken from the literature and our experiments, $P > 0.05$ for bread and durum wheat).

Comparing yield components among both types of wheat, bread wheat consistently showed to have more grains per m^{-2} than durum wheat in the dataset collected from the literature alike from our experimental dataset (Fig. 2a); and oppositely, durum wheat had consistently larger grains than bread wheat (Fig. 2b). Nevertheless, the differences in grain weight were not related to changes in the availability of resources and the ratio of grain weight between durum and bread wheat was maintained along all the environmental range explored in both the literature data and our experimental results (Fig. 2c).

3.3 Yield components in our experiments

As for the whole dataset, in average for our experiments, the weight of the grains was higher in durum (38.9 mg $grain^{-1}$) than in bread wheat (27.7 mg $grain^{-1}$). Conversely, the average number of grains was clearly higher in bread than in durum wheat (15,421 *vs*. 10,333 grains m^{-2}, respectively). Regardless of these differences, in both species yield responsiveness to environmental factors where exclusively related to changes in the number of grains (Fig. 3a) and rather independent of changes in grain weight (Fig. 3b), which in fact varied relatively little (broadly from slightly less than 20 to slightly more than 50 mg $grain^{-1}$) compared with the variation in grain number (broadly from *c*. 1,000 to more than 25,000 grains m^{-2}) (Figs. 3a,b).

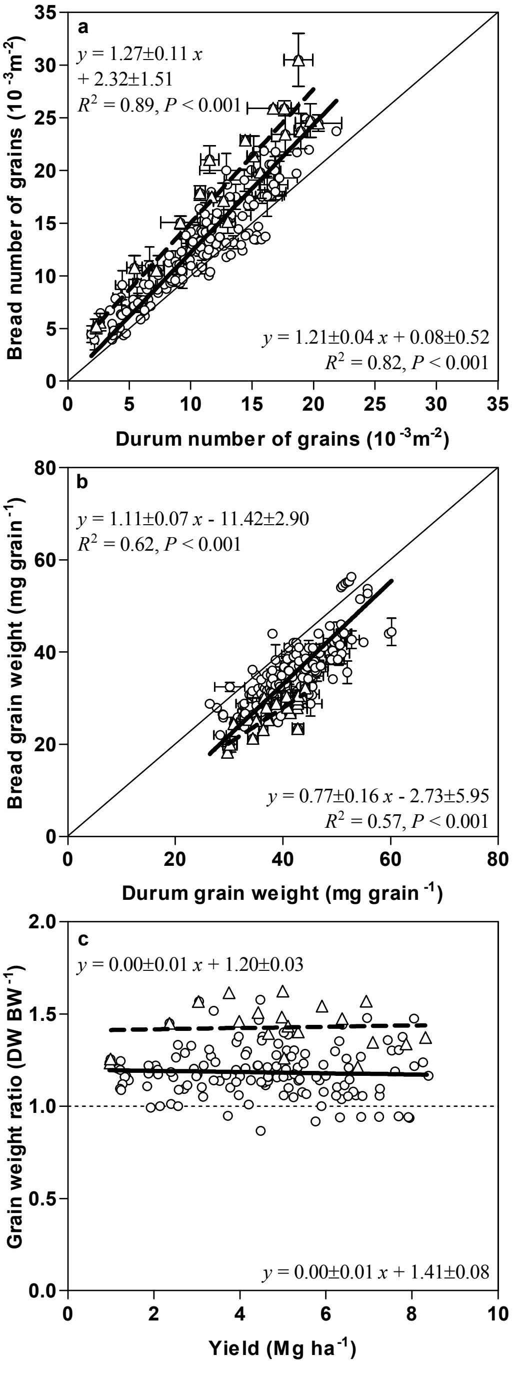

Figure 2. Pairwise comparisons between bread and durum wheat cultivars sown in the same environmental conditions for average number (a) and weight (b) of grains; and relationship between the grain weight ratio (grain weight in durum wheat divided by grain weight in bread wheat) and the average yield (c). Data for experiments carried out in NE Spain in which bread wheat and durum wheat were grown under contrasting growing conditions (triangles), and taken from published studies comparing both species of wheat (circles). Regressions (thick lines) are shown for the data set taken from the literature review (plain line) and from the experiments carried out in NE Spain (dashed line). The light lines stand for the 1:1 ratio (plain) or for cases in which grain weight was the same in both types of wheat (dashed).

In both species, the environmental effect on grain number at maturity were due to changes on the spike dry weight at anthesis (herein indirectly estimated as the dry weight of the chaff; Fig. 3c).

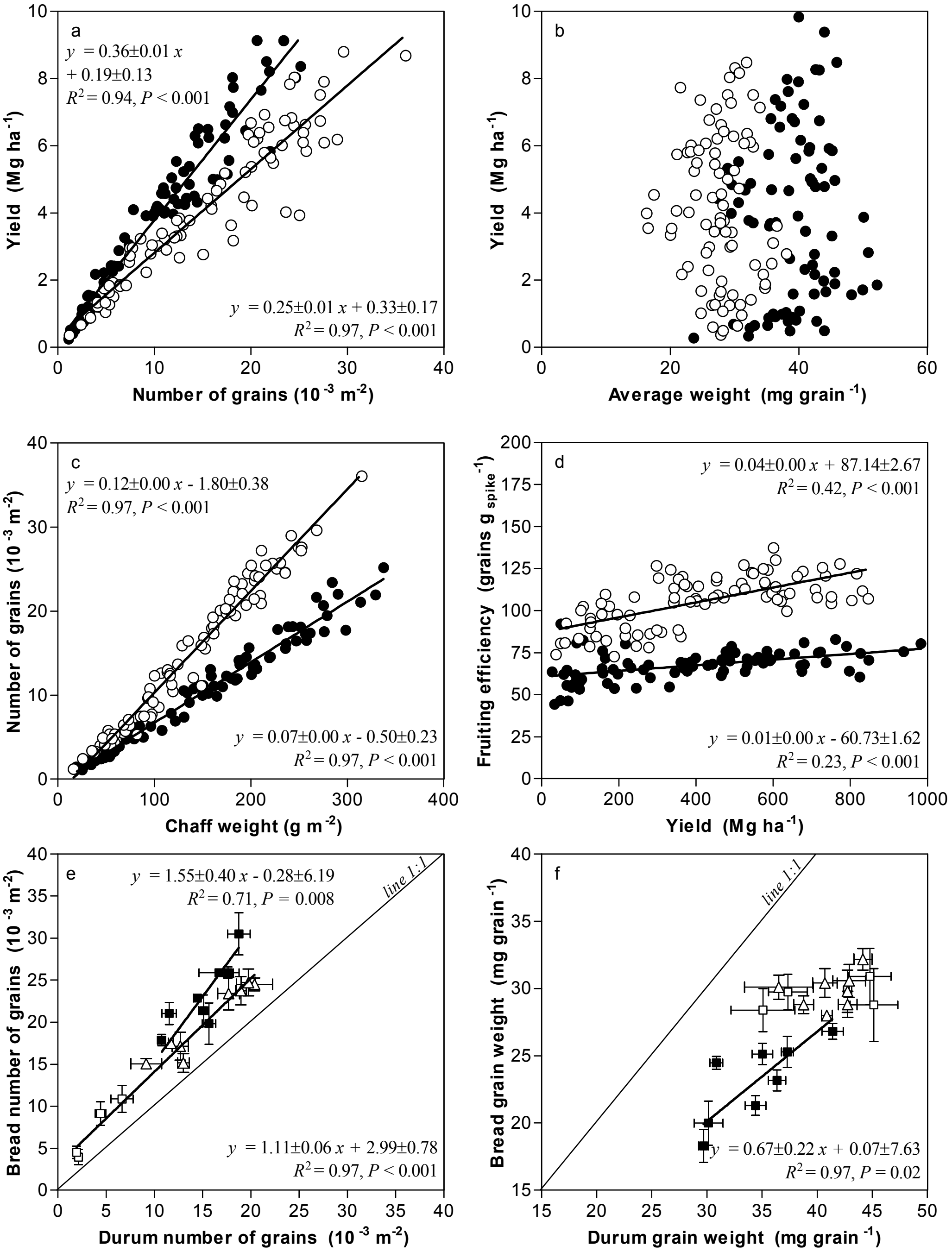

Figure 3. Relationships between yield and either number of grains (a) or average grain weight (b); between grain number and chaft weight (c), and for fruiting efficiency and the yield for durum (closed symbols), and bread wheat (open symbols) grown side by side though a wide range of conditions in different field experiments under contrasting water and N availability carried out through three growing seasons in NE Spain. In addition pairwise comparisons between durum and bread wheat from the same cultivars grown side by side for the grain number f) and the grain weight e), exp. 1 (open triangles), exp. 2 (closed squares), exp. 3 (open squares). Error bars for the pairwise comparisons, when are longer than the symbol, stand for the standard deviation of the means.

The slope of the relationship when the intercept is zero represents the average fruiting efficiency (*i.e.* number of grains set per unit of spike dry weight at anthesis) across the range of environments explored, which was significantly higher for bread (110.64±1.22 grains g_{spike}^{-1}) than for durum wheat (69.62±0.71 grains g_{spike}^{-1}) (Fig. 3c). This difference in the fruiting efficiency might be the origin of a constitutive difference in the average grain weight between the two types of wheat. In addition, despite fruiting efficiency was rather constant along the environments for both species, bread wheat responded more markedly, with steadily increments in fruiting efficiency to the increments of the environment potential than durum wheat, despite both fits were significant ($P < 0.0001$) (Fig. 3d). Oppositely, durum wheat varied grain weight more markedly along the environments (Fig. 3f).

Looking in further detail the pairwise relationship for the grain weight, bread wheat barely changed vs. durum weight in the exp. 1 and 2, while both wheat species co-varied in the exp.2, which had picks of high temperatures after anthesis, particularly affecting bread grain weight.

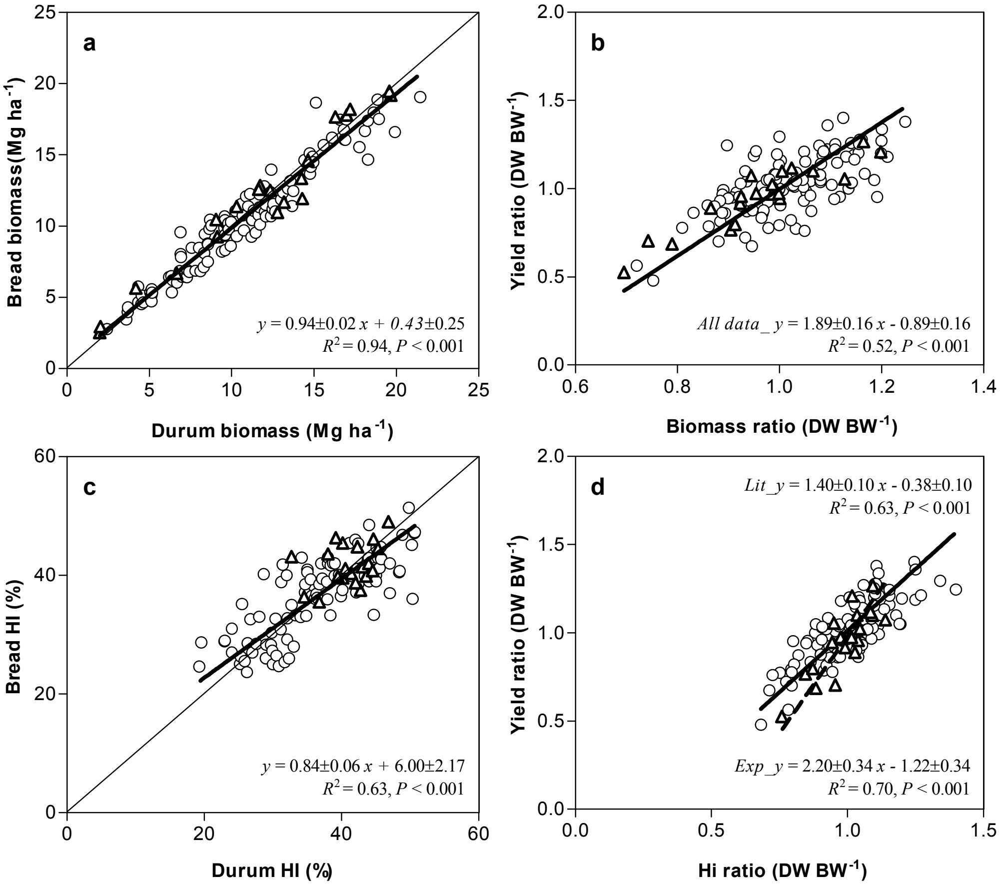

Figure 4. Pairwise comparisons between bread and durum wheat cultivars sown in the same environmental conditions for biomas (a) and HI (c) of plants; and relationship between yield ratio (durum wheat yield divided by bread wheat yield) and the biomass ratio (durum wheat biomass divided by bread wheat biomass) (b) and the HI ratio (d) for data from durum and bread wheat grown side by side though a wide range of conditions in Agramunt, NE Spain.

3.4 Biomass and HI interaction with the yielding environment along the dataset

Comparing the data from both species side by side for the whole data set, papers reporting biomass and our experimental data, both species presented similar amounts of biomass along the environments ($R^2 = 0.94$) and the slope 0.94 was not significantly different than one (Fig. 4a), contrastingly the variations in biomass between the species, estimated as the ratio (durum bread^{-1}) for the biomass, regardless of the environment, significantly explained an important fraction of the relative variation in yield ($R^2 = 0.52$) estimated as the ratio (durum bread^{-1}), (Fig. 4a).

The comparison between species on the biomass partition to yield, the HI, presented a smaller coefficient of determination ($R^2 = 0.63$) than for the total biomass, but contrastingly, the slope = 0.84, was significantly lower than one and the relationship was crossover (Fig. 4c). In addition, the relative species variation in HI, as for the biomass, explained an important proportion of the variation in yield ($R^2 = 0.63$ and $R^2 = 0.70$ for the literature and our experiments, respectively) (Fig. 4d). Contrastingly, almost no variation in yield was related to the variation of the stalk biomass $R^2 = 0.03$, either in the literature or in our experimental data (data not shown).

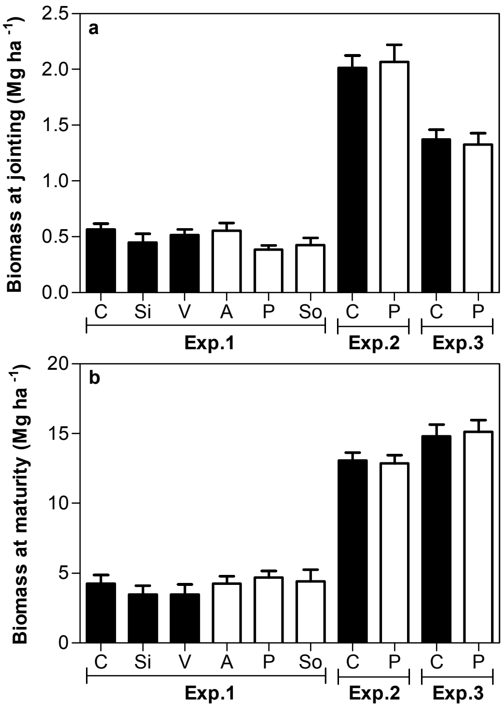

Figure 5. Biomass of durum wheat (closed bars) and bread wheat (open bars) grown side by side through a wide range of conditions in each of the three experiments carried out at Agramunt, NE Spain at jointing a), at maturity b). In panel (a) the initials stand for the cultivars Claudio (C), Simeto (Si), Vitron (V), Anza (A), Provinciale (P), Soissons (So). Error bars stand for the standard error of the means.

3.5 Differences in crop growth and total biomass in our experiments

As expected, the diverse environmental range generated important differences in total biomass at maturity (Fig. 5b). The first experiment had the lowest biomass production, *c*. 4 Mg ha^{-1} in average along the treatments, and durum cultivars presented the lowest biomass, though from those Claudio (4.2 Mg ha^{-1}) was the most productive, while among the bread wheat was Provinciale (4.7 Mg ha^{-1}) which had significantly higher biomass than Simeto and Vitron ($P < 0.05$, LSD). In the second experiment, biomass was 3 times greater than in first experiment (*c*. 13 Mg ha^{-1}) and durum slightly overproduced bread wheat along the environments, thought not significantly. In the third experiment, biomass was significantly higher than in the second experiment as a consequence of the high rainfall along SE, but again in this last experiment the average biomass along all the treatments was rather similar for both wheat species.

Taking the biomass generated until the moment of jointing, as a proxy of the earliness in biomass generation, a important relationship was found between biomass at jointing and at maturity ($R^2 = 0.5$) (Fig. 5a), despite the low amount of biomass generated until that period, the proportion of final biomass already accumulated by jointing ranged from *c*. 9 % in the irrigated conditions of exp. 3 up to 18% in the dry rainfed conditions of exp. 1. For the exp. 1, the durums generated in average a slightly higher amount of biomass at jointing (51 g m^{-2} vs. 45 g m^{-2}) though differences were only significant against Provinciale and Soissons. In exp. 2 and 3, differences were not significant though in the exp.2 with the highest biomass production by jointing bread produced in average slightly more and oppositely in exp. 3, with lower biomass, durum overproduced bread.

Observing in detail the crop growth curves after jointing some differences in their development arise (Fig 6), as expected from the cultivars description cycles, which despite to be similar present some few differences in their precocity description (*v.g*. GENVCE, 2015; http://www.magrama.gob.es). In the harsh rainfed conditions from exp. 1, where the relationship between duration and biomass was high (Fig 7c), Vitron and Soissons were the cultivars with an earlier cycle; however, that was not an advantage in the final biomass since some rains arrived after anthesis favouring the cultivars that could extend growth duration.

Contrastingly, the bread wheat Provinciale and Anza had the longest growth durations and the highest final biomass. In the irrigated conditions of exp. 1 durum wheat species started and finished crop growth earlier than bread wheat species, thought the differences in biomass where small compared to the rainfed conditions (Fig. 6b). In exp. 2, growth duration under rainfed conditions was shortened in thermal time respect the irrigated treatments, probably as a consequence of the higher temperatures of that year; in that particular conditions, the durum cultivar Claudio was slightly favoured in since it presented some earliness vs. Provinciale, while in the irrigated conditions the growth and the final biomass were rather similar. The exp. 3, which had recurrent rains from Terminal Spikeled (TS), produced small differences between the irrigated and rainfed treatments (15.97 vs. 14.79 Mg ha^{-1} respectively) thought significant ($P = 0.02$), though in contrast the N treatment was highly significant ($P < 0.0001$), producing important differences in biomass (18.40 vs. 11.54 Mg ha^{-1}, respectively). Regarding the developmental differences between the wheat species, despite final biomass was fairly similar for each treatment, bread wheat increased the crop growth rate *vs*. durum, particularly in the fertilized conditions, while durum *vs*. bread presented longer durations of growth (Fig. 6d).

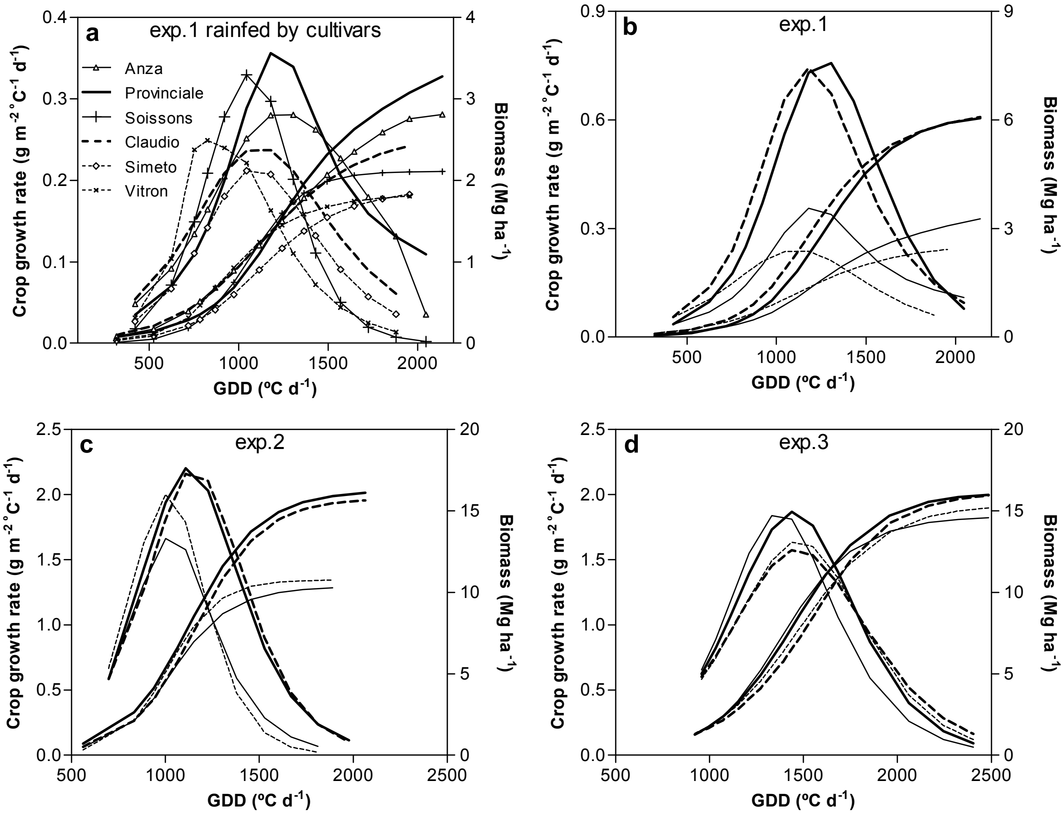

Figure 6. Dynamics of the crop growth rate (left bar scale) and the biomass (right bar scale) in thermal time for the rainfed treatment of exp.1 divided by cultivars a), for the rainfed and irrigated treatments of the exp. 1 b), for the rainfed and irrigated treatments of the exp. 2 c) and the the rainfed and irrigated treatments for exp. 3 d). For bread wheat cultivars (plain lines) and durum wheat cultivars (doted lines) grown side by side. In b, c and d, for the rainfed (thin lines), irrigated (thick lines).

From the parameters describing the curves of biomass accumulation, the maximum crop growth rate was the more correlated with the biomass at maturity ($R^2 = 0.83$), which in our dataset presented a rather linear relationship with the biomass until *c*. 2 g m^{-2} ºC^{-1} d^{-1} when further increases in rate were not related with biomass increases (Fig. 7a, fittings did not differ significantly and bread and durum wheat were fitted together). Furthermore, the relative variations between species in maximum crop growth rate explained an important amount of the variation in biomass ($R^2 = 0.47$, Fig. 7b). The thermal time of crop active growth duration, estimated here as the thermal time between the generation of 5% to the 95% of the total biomass weight, overall the experimental conditions was poorly related with biomass (Fig. 7c) and the relationship was not significant. As a consequence, its variation along the average of the treatments was not related with the variation of biomass from wheat species (Fig. 7d), though, it presented important differences between seasons, *e.g*. the growth duruation in exp. 2, which had the highest temperatures during SE, lasted in average *c*. 300 ºC d^{-1} less than in exp. 3 to complete growth; and in some particular conditions, the biomass and the active crop growth duration, presented significant relationships as depicted in the Fig. 7c which show the significant relationships for the different treatments grouped by significance, *v.g*. the rainfed conditions from the exp. 1, where rains arrived late in the season, extended the duration of some cultivars growth and a significant relationship was found between the crop active growth duration and the biomass produced for bread wheat ($R^2 = 0.63$) which increased 0.13 Mg ha^{-1} per ºC d of extended duration.

The parameters, rate and duration, were negatively related, and the slope from their relationships increased with the more favourable conditions (Fig. 7e), and therefore increases of biomass due to improvements in growing conditions were the product of maintaining growth duration while increasing the growth rate, that was the case of the N treatment in exp. 3 which significantly increased the maximum crop growth rate and the active growth duration. In addition, N treatments significantly increased the maximum crop growth rate in all the experiments, though slightly shortened the active crop growth duration in exp. 1 and 2, which were dryer; while the irrigation treatments, generated in pre-anthesis the highest maximum crop growth rate but the smallest in post-anthesis for exp. 2 and 3, while in contrast the post-anthesis irrigation extended the active crop growth duration relatively to the irrigation in pre-anthesis (45 and 186 ºC d, respectively for exp.2 and 3). Nonetheless, both species responded similarly reducing active crop growth duration with increases in the rate.

Considering the thermal time from sowing until maximum crop growth rate and the total time to complete the biomass growth (T) both timings where highly related ($R^2 = 0.84$), and a higher relationship from that duration, than that for the active crop growth, with the total biomass was present ($R^2 = 0.14$ and 0.59, respectively for T and the thermal time to maximum crop growth rate). However, only considering the post-anthesis biomass all the duration variables were significantly related with that biomass; and a particularly important part of the relative variation between species to the post-anthesis biomass ($R^2 = 0.79$) was found for T and the time to maximum crop growth (Fig. 7h); however, again, the active growth duration only explained a small part of the post-anthesis biomass ($R^2 = 0.19$).

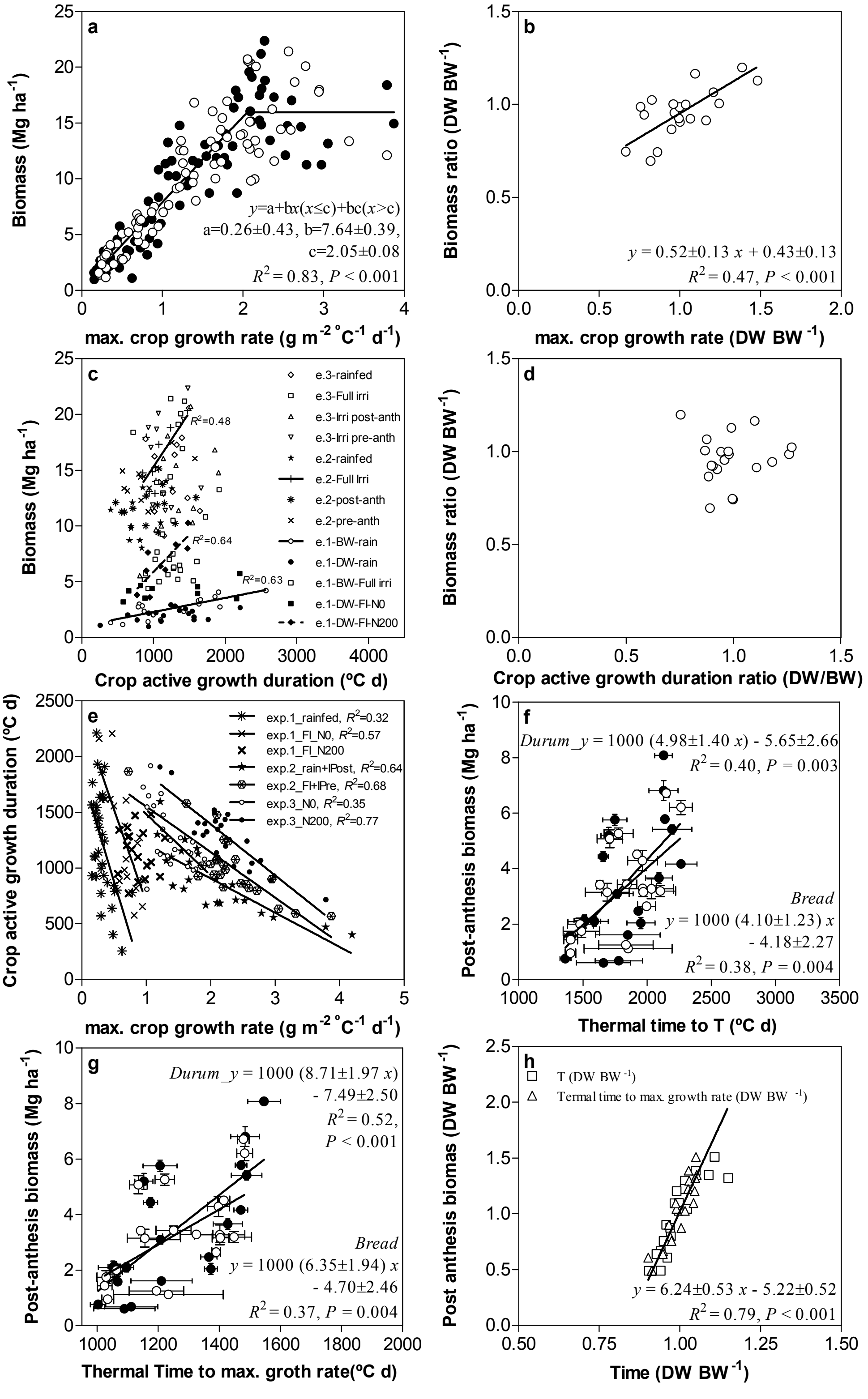

Figure 7. Relationship between the biomass and either the max. crop growth rate a), the crop active growth duration c), the thermal time to maturity (T) f), or the thermal time to max. crop growth rate g); bread wheat (open symbols), durum wheat (closed symbols). Additionally, relationships for the biomass ratio (durum bread^{-1}) and either the max. crop growth rate b), or the active growth duration ratio (durum bread^{-1}); the crop active growth duration and the max. crop growth duration e), and the post-anthesis biomass ratio (durum bread^{-1}) and the termal time ratio for T and max. crop growth rate h) are shown. Error bars for the pairwise comparisons, stand for the standard deviation of the means.

4. Discussion

Regarding the yield components "per se" approach, the wheat species presented differences in both yield components (grains per m^{-2} and average weight of the grains). Bread wheat produced more grains per m^{-2} of lower average weight than durum wheat, which seems to be a constitutive difference between the species. As expected from evolutionary and breeding reasons the number of grains responded more markedly to changes in environmental conditions than the average grain weight in both species (Peltonen *et al*., 2007; Sadras, 2007; Sadras and Slafer, 2012). The basis for the constitutive differences in grain size and grain number might be the differences in fruiting efficiency, the number of grains produced per unit of spike dry weight at anthesis. Higher fruiting efficiency may result in smaller florets and the size of the ovaries at anthesis may determine grain size potential (Calderini *et al*., 2001). This negative relationship for grain weight has been found between cultivars of durum wheat differing in fruiting efficiency (Ferrante *et al*., 2012). In fact, Gambín and Borrás (2010) hypothesised that the major driver of differences between crop species in grain size would be the number of grains set per unit of growth at the period of grain number determination.

Furthermore in our experiments in Lleida grain weight seemed to change more markedly in durum than in bread wheat (as the slope of the relationship of this component in bread *vs*. durum wheat was significantly lower than 1). This could be in line with differences in grain weight stability between both species reported (*e.g*. Palumbo and Boggini, 1994; Zubaidi *et al*., 1999; Cossani *et al*., 2011); however, not to differences in grain weight reduction as a consequence of high temperatures, since the exp. 2 with high temperatures around anthesis reduced more markedly the grain average weight of bread wheat, this could be related with the relative superior capacity to have good yields with high temperatures around anthesis for some durum cultivars (Trethowan *et al*., 2001; Reynolds *et al*., 2004), in addition an interesting interaction with the N availability was found, the heavily fertilized treatments reduced more markedly the grain size, which could be in line with N x temperature interactions found for other species (Zahedi *et al*., 2004; Passarela *et al*., 2008; Ordoñez *et al*., 2015). However, another explanation for the differences in grain weight stability could be that durums adjust in a higher degree sink-size to the availability of resources with that yield component, since their variation in grain number through the environment was lower.

Regarding the biomass approach, both species produced similar amounts of biomass along the environments, which however presented important variation in its dynamics mainly between cultivars, rather than between species. And therefore the cross-over yield interaction with the environment was not strictly related to variations in total biomass but to differences in HI, which additionally presented a significant cross-over interaction. Nonetheless, the species differences in yield were highly related to differences in biomass and HI, and contrastingly not related with the variation in stalk biomass from the plants; a plausible explanation could be that the variations of biomass yield, though relevant in yield terms, were rather small in comparison with the total biomass generated. Further support to that assumption is the significant enlargement in crop growth duration with the relative species higher post-anthesis biomass, since positive associations have been found between crop growth rate and duration and biomass accumulation in post-anthesis, as a consequence of differences in sink-strength (Reynolds *et al*., 2007; Lopes and Reynolds, 2012).

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Chapter IV: Sink-strength determines differences in performance between bread and durum wheat

Abstract

It is frequently assumed that durum wheat can yield better under stress than bread wheat. However, recently in a large comparison of experimental and literature data along a wide range of environmental conditions, a cross-over interaction of yield from bread *vs*. durum wheat was found. Nonetheless, opposite to that expected bread outyielded durum wheat in the low-yielding conditions while durum wheat tended to have higher potential yield. I aimed to test whether the species cross-over difference in yield performance was established before or after anthesis and to determine if it was related with differences in sink-strength. Our study indicates that the consistent species-by-environment interaction for yield is the consequence of few characters related to sink-strength and determined around anthesis. Thus, differences in the spike weight and N accumulated at anthesis, which produced important variations in the number of grains, and presumably generated differences in sink-strenght appear involved. This conclusion is supported by the strong relationship between grain yield and the biomass produced during grain filling, in addition to the fact that the variation in individual grain weight, as well as its rate or duration of grain filling, was poorly related to yield and the post-anthesis biomass.

Keywords: Bread wheat; durum wheat; grain yield; sink strength, post-anthesis biomass, yield components.

1. Introduction

A common approach to raise yield of crops is through gains in yield potential, which ultimately have demonstrated to generate relative increases of yield in most of environments (Richards, 1992; Calderini and Slafer, 1999; Trethowan *et al*., 2002; Slafer and Araus, 2007; Marti and Slafer, 2014). However, crop performance is not only a function of the genotype but of the environment where it is to be expressed (Fischer and Maurer, 1978; Blum, 2005; Marti and Slafer, 2014), precluding a direct extrapolation of the potential yield gains to actual yield and highlighting the need for understanding the genotype by environment (G x E) interactions. That information will ultimately help to design strategies to effectively increase field crops productivity.

In Chapter II, we found evidences that the traditional land allocation from two of the more commonly used species of wheat, bread wheat (*Triticum aestivum* L.) and durum wheat (*Triticum turgidum* L. ssp. *durum*), was opposed to their productivity responsiveness to environmental conditions. Bread wheat yielded more under low-yielding conditions while durum wheat exhibit a higher yield potential, being that crossover in the G x E interaction generally independent from the experiment or the cultivars used.

Unfortunately, little is known about the causes producing the G x E interaction for yield between bread and durum wheat, and the understanding and extrapolation of literature results is not straightforward. Some differences among cultivars of bread and durum wheat have already been identified; durum wheat seems to have less pre-anthesis growth than bread wheat, affecting the number of grains set, in the drought prone areas of Australia (Zubaidi *et al*., 1999), for which it would require higher radiation and cooler average temperatures in the period to produce a similar grain number (Reynolds *et al*., 2004). These differences may well be a consequence of the constitutively heavier kernels of durum wheat (Chapter III), since the differences in the capacity of setting a certain number of grains and the potential size of the grains may imply differences between both species in sink-strength after anthesis, and this strength may be relevant for determining yield (Serrago *et al*., 2013).

It seems also that durum wheat presents less yield stability when exposed to terminal drought (Zubaidi *et al*., 1999; Chinnusamy and Khanna-Chopra, 2003); although in some experiments it was found that durum cultivars were well adapted to the post-anthesis warm conditions (Zhang and Oweis, 1999; Reynolds *et al*., 2004) and to maintain photosynthesis (Dias *et al*., 2011) and grain filling (Dias and Lidon, 2009) under heat stress. In this study I aimed to determine whether differences in performance between durum and bread wheat across a range of environmental conditions were established before or after anthesis and in the latter case if this is related to the establishment of certain differences in sink-strength at around anthesis. The basic hypothesis is that the consistent species-by-environment interaction for yield is the consequence of few characters determined around anthesis related to sink-strength and not to differences in grain filling, rate or duration.

2. Materials and methods

To achieve the objective of this Chapter I further analyzed the field experiments reported in Chapter II, in addition to the weekly samplings of biomass reported in Chapter III separated into stems (plus leaf sheaths), leaf lamina, spikes (from booting onwards) and grains (in post-anthesis) oven-dried for 3 d at 60 ºC and weighted.

The raw data of variables measured weekly were adjusted for each experimental unit by non-linear regression to a logistic curve against accumulated thermal time, calculated as the sum of daily average temperature [(Tmax+Tmin)/2] with a base of 0 ºC (e.g. Hay and Kirby 1991; Calderini *et al*. 1996). The NLIN procedure (SAS Institute, 1999) was used and all relationships where highly significant ($R^2 > 0.90$; $P < 0.001$). For the grain filling analysis, the procedure described in Darroch and Baker (1990) was followed to analyse the parameters of the logistic curves (Chapter III); however, the grain filling average rate was counted by dividing the total grain yield by the thermal time to fill the grains (from the onset of grain filling, at the end of the lag phase, to physiological maturity) while the individual grain filling rate was calculated with the same procedure but replacing the total grain yield for the average individual grain weight. Data from the biomass fits was divided in two periods, accumulated up until anthesis (pre-anthesis biomass) and accumulated from the moment of anthesis onwards (post-anthesis biomass).

Pairwise comparisons from bread and durum wheat were analyzed using regression analyses. In all the analyses when regressing a variable in bread wheat against the same variable in durum wheat both variables were subjected to error, thus I fitted the regressions with Model II (Ludbrook, 2012).

3. Results

The comparison between yields from both species across the wide range of conditions of this study, earlier discussed in Chapter II, presented a crossover interaction with the environment, being the regression lines from bread and durum wheat yields with the environmental index significantly different ($P = 0.004$). In the poorer conditions (*c*. 2 Mg ha^{-1}) bread wheat yielded more than durum wheat and contrastingly durum wheat yielded more in the highly yielding conditions (*c*. 8 Mg ha^{-1}) than bread wheat, being the species difference *c.* 0.5 Mg ha^{-1}for both conditions. This crossover interaction was the consequence of durum wheat being more responsive (i.e. less stable) to changes in the environmental conditions than bread wheat. Differences in yield between both species across the environments, were the consequence of differences in their biomass ($R^2 = 0.85$, $P < 0.001$), and differences in HI, which also explained in part differences in yield ($R^2 = 0.70$, $P < 0.001$). The stalk yield, the remaining non grain part of the biomass at maturity, was similar for both species.

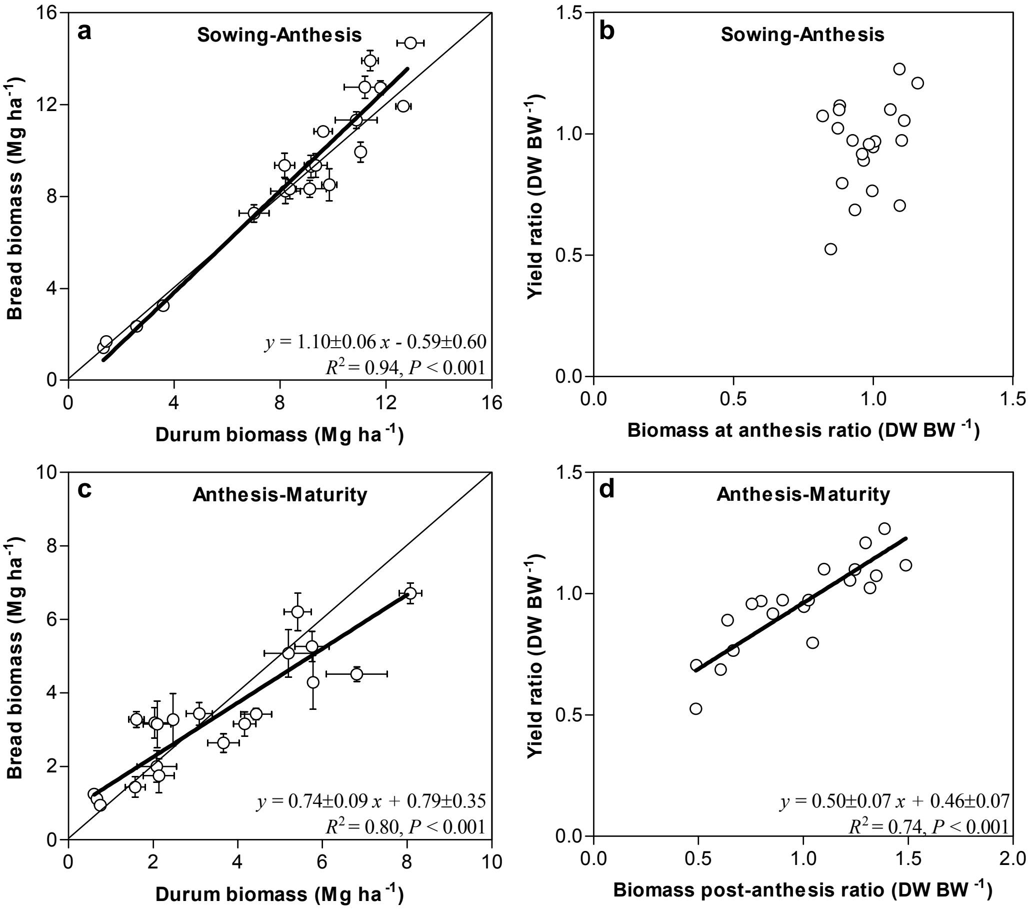

Figure 1. Pairwise comparisons between durum and bread wheat biomass accumulated up to anthesis (a) or between anthesis and maturity (c); and the relationships between the yield ratio (durum wheat yield divided by bread wheat yield) and either the ratio (durum wheat divided by bread wheat) of biomass accumulated up to anthesis (b) or after anthesis (d). Durum and bread wheat were grown side by side thorugh a wide range of conditions in NE Spain. Light lines in panels a and c represent the 1:1 ratios and thicker lines were fitted by regression analyses, whose equations are also included (whenever the relationship was significant). Error bars, when longer than the symbol, stand for the standard error of the means (SEM).

3.1 Biomass production before and after anthesis and the relevance for yield determination

Before anthesis both species produced a wide range of biomass (*c.* 1-15 Mg ha^{-1}). In that period bread wheat tended to produce slightly more than durum in the plots fertilized and with high water availability from the second and third seasons. However, in general, for the whole pre-anthesis biomass dataset, durum and bread wheat had similar values across the range of environments explored (Fig. 1a). In fact the regression line between the biomass accumulated up to anthesis by bread and durum wheat was not significantly different from the 1:1 line. Therefore, the differences between the two species in pre-anthesis biomass was firstly much smaller than the differences in yield and secondly not related to differences in yield ($R^2 = 0.09$; Fig. 1b).

The biomass produced after anthesis across the environments presented a narrower range than that produced before anthesis (*c*. 1-8 Mg ha^{-1}; Fig. 1c). Rainfed and unfertilized treatments from the first season had the lowest post-anthesis biomass and the irrigated and fertilized treatments from the third season had the highest ones. Comparing biomass accumulated after anthesis between bread and durum wheat evidenced a crossover interaction, as the coefficient of regression was significantly lower than 1 and the intercept positive, implying that under low-yielding conditions bread wheat accumulated more biomass than durum wheat after anthesis and the opposite was true in high-yielding environments (Fig. 1c). In addition, the differences in post-anthesis biomass between the two species explained an important proportion (almost 75%) of their differences in yield (Fig. 1d).

3.2 Yield components, yield and biomass generated in post-anthesis

In both species the number of grains was the main component explaining yield along the explored environmental range ($R^2 = 0.94$, $P < 0.001$; and $R^2 = 0.97$, $P < 0.001$ for bread and durum wheat, respectively) and contrastingly in none of them yield was significantly related to the average size of the grains ($R^2 = 0.01$, $P > 0.05$ for durum wheat and for bread wheat). Bread wheat consistently had more grains per m^{-2} than durum, while durum wheat had consistently larger grains than bread wheat along all the environmental range explored. Nonetheless, the gap in number of grains produced by bread wheat respect to durum wheat decreased in magnitude along the increase of yielding conditions of the environments, and therefore, the proportion of grains being produced by durum wheat *vs*. bread wheat continuously increased along the environments (from *c*. 0.4 to 0.9).

The differences in yield between the two species along the gradient of yielding conditions explored was more strongly related to the differences in the number of grains between both species (Fig. 2a), than in the average weight of the grains (Fig. 2b). In addition, the relative differences between the two species in the post-anthesis biomass produced were highly related to their differences in grain number (Fig. 2c), implying that the relationship between the differences in yield and those in post-anthesis growth (Fig. 1d) may reflect the effect of yielding capacity on post-anthesis growth. The lack of relationship between the differences in biomass accumulated during grain filling and those in average grain weight (Fig. 2d) further supports that post-antheis growth may be a consequence of differences in capacity for grain set around anthesis rather than a driving force for the differences in yield.

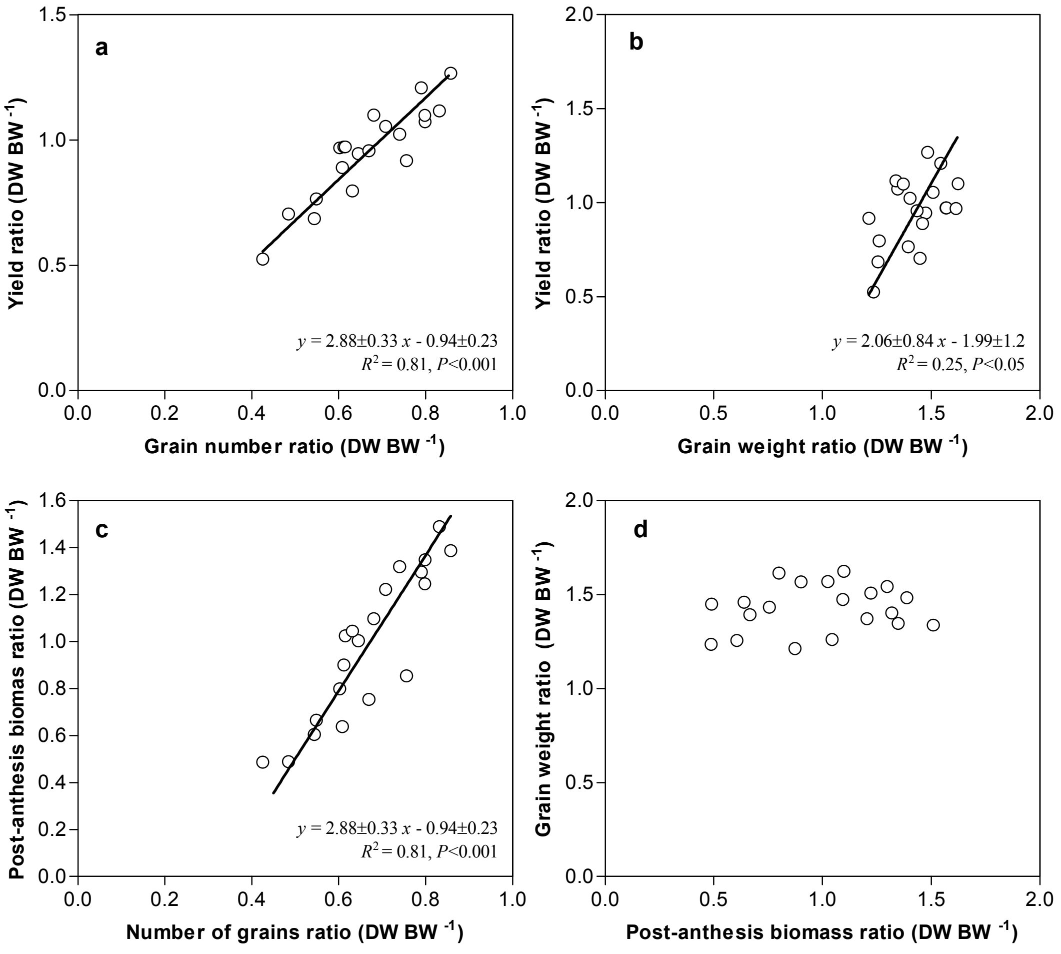

Figure 2. Relationships between: (i) grain yield ratio and either the grain number ratio (a) or the grain weight ratio (b); (ii) the post-anthesis biomass (biomass accumulated from anthesis to maturity) ratio and the grain number ratio (c); and (iii) the grain weight ratio and the post-anthesis biomass ratio (d) from experiments in which durum and bread wheat were grown side by side through a wide range of conditions in Agramunt, NE Spain. In all cases the ratios were calculated as the durum wheat divided by the bread wheat values.

3.3 Spike dry weight at anthesis determining yield components and post-anthesis crop growth

The variation in spike dry weight at anthesis (estimated from chaff weight) explained most of the changes in the number of grains for each of the durum and bread wheat species separately ($R^2 = 0.97$) (Chapter III). Comparisons between both species in chaff weight were similar to those in yield: the relationship between chaff weight of bread *vs.* that of durum wheat evidenced a crossover interaction with the environment potential (Fig. 3a); as the slope was significantly lower than 1. Expectedly such differences in chaff weight explained an important part of those in grain number (Fig. 3b) and contrastingly there was almost no relationship between the differences in chaff weight and those in average grain weight ($R^2 = 0.06$). It seemed that the differences in post-anthesis growth between the two species were the consequence of the differences in spike dry weight at anthesis (estimated as chaff weight) (Fig. 3c); which ultimately determined differences in yield (Fig. 3d).

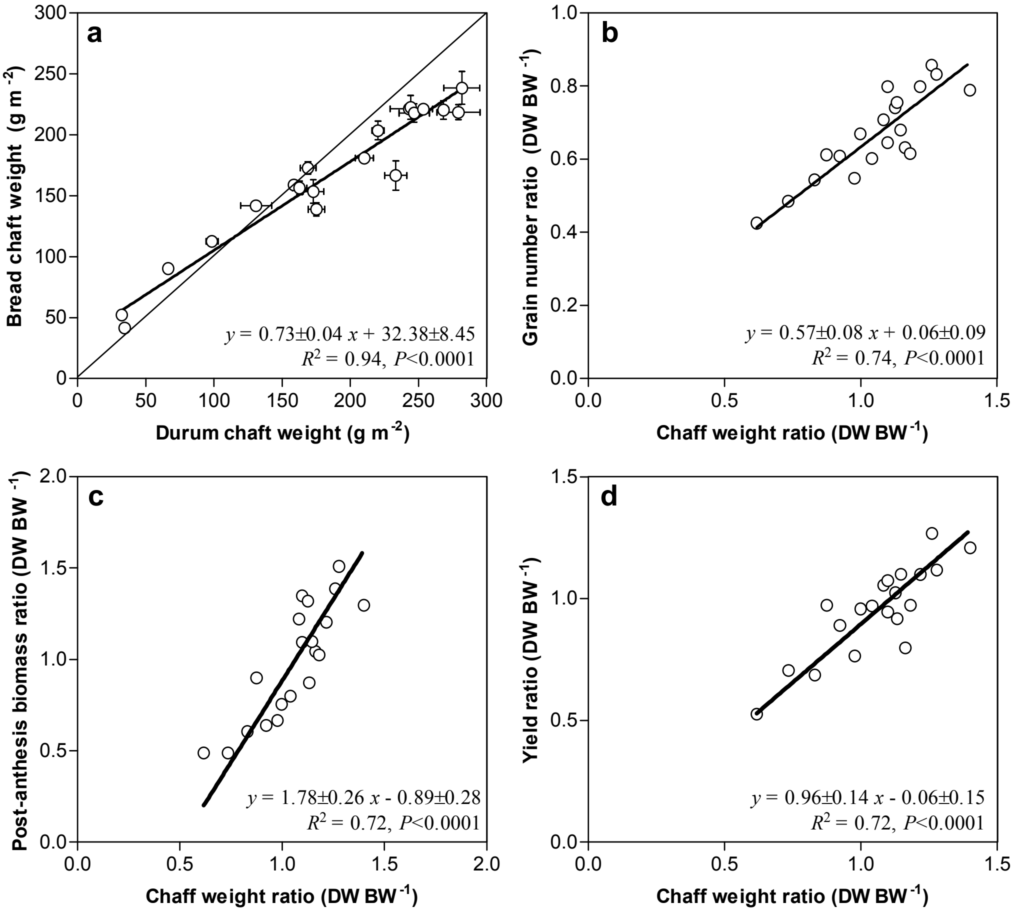

Figure 3. Pairwise comparisons between durum and bread wheat cultivars grown side by side through a wide range of conditions in Agramunt, NE Spain, for chaff weight (a) where the thin line stands for the 1:1 ratio. The relationship is accompanied with the relationship between the chaff weight ratio and the grain number ratio (b), the post-anthesis biomass ratio (c) and the yield ratio (d). In all cases the ratios were calculated as the durum wheat divided by the bread wheat values. The thick lines and the equations stand for the regression analysis. Error bars when longer than the symbol stand for the standard error of the means (SEM).

3.4 Relative growth and partition to spike around anthesis

Although differences between these two species in total pre-anthesis growth were not clear (Fig. 1a), those in biomass accumulated from 20 d before to 10 d after anthesis (which is the named critical period for grain number and yield determination in wheat; Savin and Slafer, 1991) presented a crossover interaction (Fig. 4a). The differences between the two species in biomass accumulation during this critical period were tightly related to differences in yield (Fig. 4b). As these differences in biomass were related to chaff weight (R^2 = 0.55), differences in growth during the critical period may be the driving force behind the relationship between differences in chaff weight and those in yield (Fig. 3d). Although most of the differences between the species in yield were explained by differences in growth around anthesis, there was also a contribution of the differences in partitioning (i.e. during grain filling) through the growing of juvenile spikes (Fig. 4c).

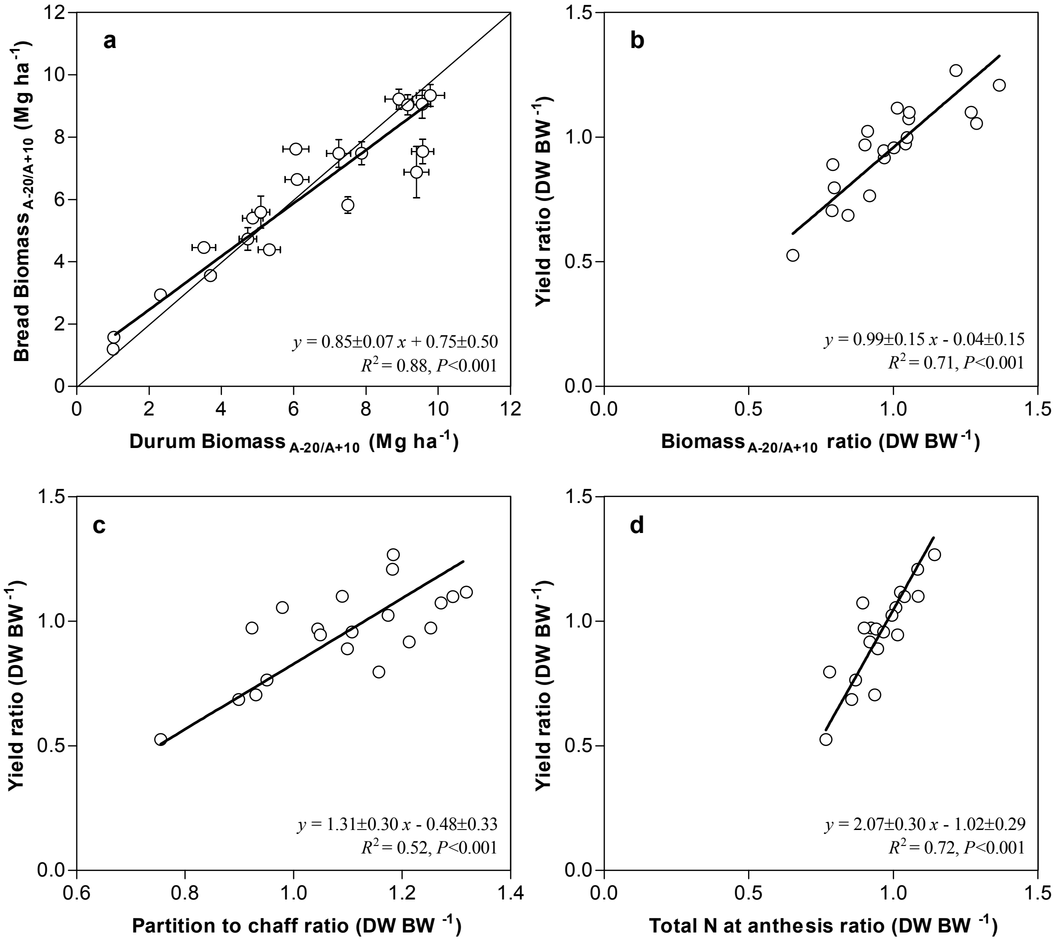

Figure 4. Relationship between the generated biomass around anthesis (*i.e.* biomass accumulated between 20 d before [A-20] and 10 d after [A+10] anthesis) in bread wheat compared with durum wheat (a) and the relationship of the grain yield ratio against the ratio of the biomass accumulated around anthesis (b), the ratio of the biomass partition to chaff at maturity (c) and the ratio of total N uptake at anthesis (d). In all cases the ratios were calculated as the durum wheat divided by the bread wheat values. Durum and bread wheat were grown side by side through a wide range of conditions in NE Spain. Error bars, when longer than the symbol, stand for the standard error of the means (SEM).

Regarding the N economy at anthesis, the differences in total N absorbed presented an interaction with the yielding environments. Thus, despite that total biomass at anthesis was very similar for the two species across the large range of environmental conditions (Fig. 1a), the two species differed in the amount of N absorbed and the differences in N uptake at anthesis were significantly related to that in yield (Fig. 4d).

3.5 Differences in time and rate to fill the grains and its relationship with yield

After anthesis the average time to fill the grains was very similar for both species of wheat in each of the environments. Consequently, the slope of the relationship between grain filling duration of bread and that of durum wheat was not significantly different from 1 (Fig. 5a);

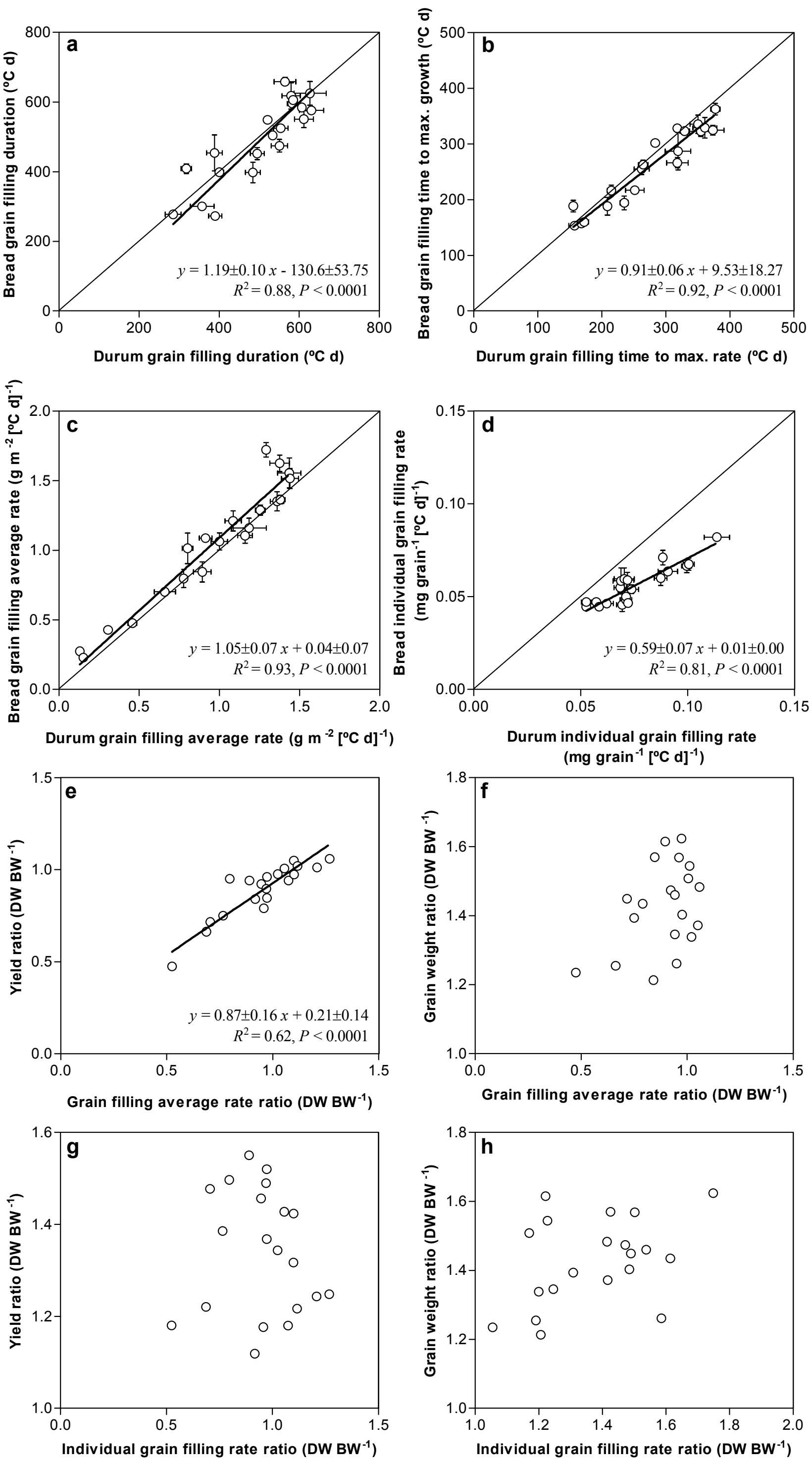

Figure 5. Pairwise comparisons between bread and durum wheat for cultivars grown in the same environmental conditions for grain filling duration (a), time from anthesis to maximum rate of filling (b), for grain filling average rate (c), and for the individual grain filling rate (d). Additionally, the relationship between the grain yield ratio and the ratio for the average grain filling rate (e) and the ratio in individual grain filling rate (g), and the relationship between the individual grain weight and the ratio for the average grain filling rate (f) and the ratio in individual grain filling rate (h) are depicted. In all cases the ratios were calculated as the durum wheat divided by the bread wheat values. Durum and bread wheat were grown side by side through a wide range of conditions in NE Spain. Error bars, when longer than the symbol, stand for the standard error of the means (SEM).

and the duration to reach the maximum rate of grain filling was also similar for both species across the different environments (Fig. 5b). Considering the whole population of growing grains, the average rate of grain filling (per land area unit) was similar for both wheats (Fig. 5c) despite that it tended to be (not significantly) higher in bread than in durum wheat. However, considering one grain regardless of grain number, the individual rate of grain filling was clearly higher for durum, and presented an slope smaller than one (Fig. 5d).

Expectedly, as differences in yield were more related to those in grain number than in average weight of the grains, the differences in average rate of grain filling of all grains together was significantly related to the differences in yield (Fig. 5e), whereas no relationship was found between the differences in grain filling rate (per unit land area) and those in average grain weight (Fig. 5f), or for the individual grain filling rate and the yield or the average grain weight (Fig. 5g,h).

4. Discussion

The crossover yield interaction between bread and durum wheat found along the wide environmental range of our experimental conditions (chapter II), was mainly generated as a result of differences in the biomass produced after anthesis, and despite the total biomass generated until anthesis was fairly similar between the two species. There are only few literature results compatible with the data available in this thesis, but in many cases they agree with this finding. For instance, Aggarwal *et al.* (1986) found similar pre-anthesis biomass in a large comparison of bread and durum wheat cultivars while most of the differences between the species where found in post-anthesis. Zubaidi *et al.* (1999) also reported that most of the differences between these two wheat were generated during grain filling. This is not surprising, as many evidences suggest little variability in pre-anthesis biomass (Austin *et al.*, 1980; Slafer *et al.*, 1990) or its rate of production (Calderini *et al.*, 1997) among historical and more recently released commercial wheat cultivars sown in the same environmental conditions.

Despite that post-anthesis differences in biomass were well related with those in yield, our interpretation of this relationship was not that the difference in growth capacity at the timing of yield realisation was relevant for determining yield, but the other way around: the differences established in potential yielding capacity brought about parallel differences in post-anthesis growth. Thus, post-anthesis differences in biomass were mainly determined by differences in grain number; in turn determined by differences in spike dry weight at anthesis. As a consequence, most of the differences in yield and biomass between the wheat species were necessarily originated during the period of growth of the juvenile spikes immediately before anthesis, a period in which the grain number is largely determined (Fischer 1983; Kirby, 1988). The fact that the yield differences between the two species were mainly determined by variations in the number of grains contrast with the fact that irrespective of the environmental conditions, in almost all the comparisons the number of grains in bread wheat was larger than in durum wheat because a lower number of spikes and a smaller fruiting efficiency in durum wheat. In fact there was not a crossover interaction with the environment between durum and bread wheat for the number of grains, even when differences tended to slightly increase in the higher yielding conditions (Fig. 2a, Chapter III). However, that contradiction seems only apparent: (i) grain number in bread wheat is constitutively larger than in durum wheat (see Chapter III and references herein), (ii) the difference between both species was numerically important in the poor-yielding conditions but it tended to decrease under high-yielding conditions (*i.e.* in the poorest-yielding conditions of our experiments [*c.* 1 Mg ha^{-1}] bread wheat set *c.* 2.3 times more grains than durum wheat, meanwhile in high-yielding conditions [*c.* 8 Mg ha^{-1}] the differences were reduced to only *c.* 30% more grains and iii) the individual grain weight was in all the situations constitutively heavier in durum wheat (Chapter III).

Some authors suggested that the relatively lower number of grains produced by durum wheat is the consequence of lower efficiency in grain setting (Zubaidi *et al.*, 1999; Reynolds *et al.*, 2004) while forcing durum wheat to rely more on grain filling to achieve similar yields than bread, via increasing grain weight (Aggarwal *et al.*, 1986; Zubaidi *et al.*, 1999). However this study, together with our previous meta-analysis of literature data (Chapter II), suggest that the differences in grain number and grain weight were mainly constitutive and independent from the environmental conditions. Additionally, differences in the relative grain filling duration, slightly shorter for bread, and the rate, slightly higher for durum, also appear constitutive, which agree with the literature (López-Castañeda and Richards, 1994; Dias and Lidon, 2009). Dias and Lidon (2009), after imposing temperature treatments during grain filling, found similar reductions between both species in duration and rate of filling, despite that under the control durum wheat showed in average slightly longer durations and smaller filling rates. This could be in agreement with the fact that durum tended to mobilize slightly more assimilates from tillers (Fig. 2, Chapter V), particularly in the higher yielding conditions, in which grain number and sink strength during grain filling are maximised, and could explain a better capacity than bread wheat to sustain grain filling (Zhang and Oweis, 1999; Reynolds *et al.*, 2004; Calderini *et al.*, 2006). The higher contents of water soluble carbohydrates reported in durum relative to bread wheat supports a better performance of the former to filling the grains (*e.g.* D'Egidio *et al.*, 1998; Ehdaie *et al.*, 2006; 2013).

Additionally, other evidences found in our study also support the period of spike growth, critical for yield formation (Fischer, 1985; Slafer, 2003), as the origin of the differences between both species in growth and partition of biomass along the environments. Thus for example most of the differences between species in N absorption were already established at anthesis, presenting again a crossover interaction with the yielding environment. Since most of the N is commonly absorbed by the plant until anthesis (Dreccer *et al.*, 2003) strong associations between spike dry weight and N content at anthesis have been found (Demontes-Mainard and Jeuffroy, 2004), meaning that the differences in the total N absorbed at maturity were already mostly established at anthesis. Differences in biomass growth and partitioning and N content during that period have already been identified as the cause of differences in grain number and sink-strength (Fischer, 1985; Prystupa *et al*., 2004; Reynolds *et al*., 2005). The relative interception of the radiation between both species in post-anthesis showed an interaction with the environment (Fig. 6, Chapter VI), with differences being highly related with yield. These results further support that differences in grain number and spikes dry weight, which affected sink-strength, ultimately generated relatively more demand of the post-anthesis photosynthesis in bread compared with durum wheat (Wang *et al*., 1998; Calderini *et al*., 2006; Acreche and Slafer, 2009).

The above evidences support the idea that the differences in post-anthesis biomass where the consequence of differences in sink-strength between both wheat species; since wheat is mainly sink limited in post-anthesis (Slafer and Savin, 1994).

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Chapter V: Leaf, tillers and root traits, responses of bread and durum wheat under a wide range of environmental conditions

Abstract

Durum wheat in comparison to bread wheat, as a consequence of its restricted localization and adaptation to the Mediterranean Basin, may present some advantageous traits for the drought prone conditions. In this chapter, the relative performance for some morphological traits (leaf, tiller and root) between bread and durum wheats grown along a wide range of environments is described. As a result, bread in comparison to durum wheat produced a higher leaf area and weight by m^2 than durum, though because differences in the coefficient of attenuation, interception was rather similar; a higher number of tillers, stems and spikes, despite durum wheat presented a higher remobilization of stems mass in post-anthesis; and a lower number of roots under drought prone conditions. However, those stress traits, in contrast with the hypothesis that they would generate positive differences in biomass under stress for durum wheat, were not associated with the total biomass generated under such conditions, likely as a consequence of the lower sink-strength of durum wheat under stress.

Keywords: Triticum, ploidy, leaf, tiller, root.

1. Introduction

The convenience of having scientifically solid comparisons between durum and bread wheat has been presented (Chapter I).

However, there is little known on the quantitative differences in some morphological traits, which may be highly relevant for adaptation to stress, as described for durum in comparison to bread wheat (*e.g*. Percival, 1921; Marshal, 1987; López-Castañeda and Richards, 1994; Zubaidi *et al*., 1999; Mac Key, 2005; Araus *et al*., 2007), in particular relatively important roles have been assumed for the leaf, tiller and root traits, which could generate differences in biomass and ultimately yield along the environments. In the few comparisons available, morphologically, bread wheat was described to present a relatively a greater leaf area from the two-leaf stage onwards, producing a crop higher leaf area index (LAI) (López-Castañeda and Richards, 1994; Zubaidi *et al*., 1999) and a higher number of tillers by m^{-2} (Percival, 1921; López-Castañeda and Richards, 1994; Zubaidi *et al*., 1999). This is relevant as they may be important in determining differences in early vigour, which favoured a rapid canopy establishment to eventually generate differences in interception of radiation and biomass (Zubaidi *et al*., 1999); however, a reduced leaf area may be a positive trait for improved WUE under drought prone conditions (Araus *et al*., 2002). Contrastingly, durum wheat cultivars were found to present a longer coleoptile associated to early vigour in the emergence (Trethowan *et al*., 2001) and thicker tillers (López-Castañeda and Richards, 1994), which could be related to a higher capacity to fill the grains under stress (Shearman *et al*., 2005; Dreccer *et al*., 2008; Talukder *et al*., 2013) as a consequence of differences in remobilization of water soluble carbohydrates (WSC), found higher for durum wheat in the few available comparisons (D'Egidio *et al*., 1998; Ehdaie *et al*., 2006). In addition, durum wheat have a comparatively low tillering capacity, making durum more dependent on the early developed, deeper reaching seminal root system (Mac Key, 2005), since nodal root production, in comparison to seminal roots, has been related with the number of tillers and N fertilization response (Wang and Below, 1992) some important differences between the species in root production may exist.

Regarding the relative species root generation; kernel weight (Mac Key, 2005) and the coleoptile length (for barley, Grando and Cecarelly 1995) have been found related with the seminal root system, associated with the wheat ploidy level (Mac Key, 2005); which may be a possible stress adaptive role (Araus *et al*., 2007). However, other literature evidences show opposite results; Hurd (1964) and Zubaidi *et al*. (1999) found that durum wheat in general produced less roots associated to a bad moisture soil extraction, affecting post-anthesis grain filling; in addition to finer and highly branched roots for bread wheat, related with its superior yield stability (Zubaidi *et al*., 1999).

In this chapter I described the relative bread and durum wheat performance for those traits along the availability of resources.

2. Materials and methods

To achieve the objective of this chapter I further analyzed the experiments detailed in Chapter II, from which the weekly samples (Chapter III) were separated into stems (plus leaf sheaths), leaf laminae and spikes (from booting onwards). In post-anthesis, from the weekly measures of stem weight, the stems weight loss was calculated as the maximum fall in stem weight from its maximum value. In fresh, the area of each blade was then estimated with a photometric area-integrating meter, LI-COR Model LI-3100C, manufactured by LI. COR, Inc. Corporation. The Leaf Area Index (LAI) was calculated as the leaf area by m^2 and the specific leaf weight (SLW) as the quotient between leaf weight by m^2 and LAI. Later the samples were oven-dried for 3 d at 60 ºC and weighed. After determining dry weight of the different organs in which dry matter was determined, from the dry samples, (leaves, stems, spikes) at anthesis and (grains, and stems) at maturity total N contain was determined by the Kjeldahl method.

The amount of intercepted radiation by the crop was calculated weekly as the ratio between the difference of incident and transmitted radiation to incident radiation, measurements where made at noon only in clear days, from the appearance of the first node to maturity. Incident and transmitted radiation to ground level were measured using a 1 m long linear sensor (LI 191 S, Licor Inc., Lincoln NE, USA), to measure transmitted radiation, the line sensor was placed across the rows in a very uniform zone of the experimental unit. The interception efficiency was assessed thorough the coefficient of light attenuation (k) determined form the relationship between intercepted radiation percentage and the Leaf Area Index (LAI), and adjusted following the exponential model (1) (Jamieson *et al*., 1995)

(eq. 1) $IR\% = a(1 - \exp^{(-k(LAI-c))})$

where a is the maximum value of radiation interception, K is the attenuation coefficient and c is the LAI at which intercepted radiation is 0.

At anthesis with a root auger of 72 mm of diameter soil samples where taken in field plots until 1m deep, the samples where divided in 4 soil layers of the same volume. Soil samples were cleaned from soil and the other organic matter and, finally, the roots retained by a 0.2 mm sieve where analyzed for length with a scanner over a transparent plate inside a water lamina. The scans photographs where analyzed using the program winRhizo v.5.0A (Regent Instruments, Québec, Canada).

Data from bread and durum wheat were analyzed using regression analyses. In all the analyses when regressing a variable in bread wheat against the same variable in durum wheat both variables were subjected to error, thus I fitted the regressions with Model II (Ludbrook, 2012).

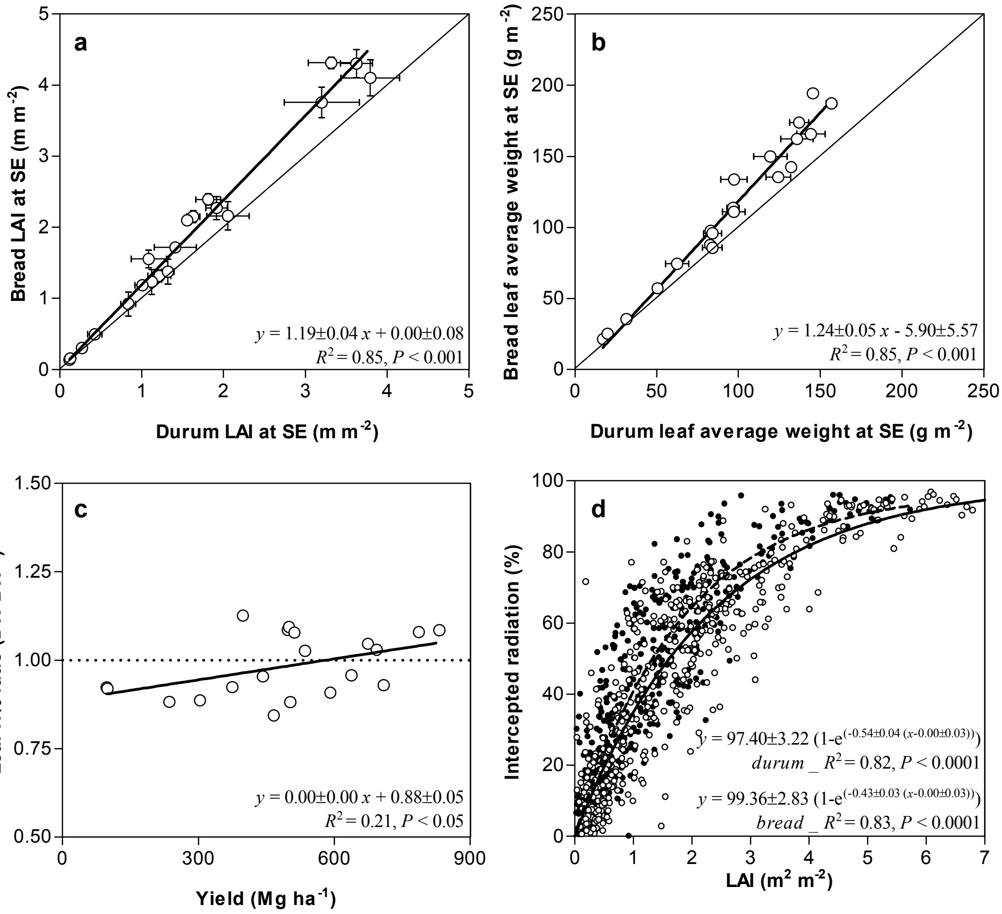

Figure 1. Pairwise comparisons between bread and durum wheat with data from the different experiments carried out in NE Spain for the LAI (Leaf area index) at stem elongation (SE) a) and for the average leaf weight at SE b) and relationship for the leaf N concentration (%) ratio (durum wheat divided by bread wheat leaf N concentrations) at anthesis c) and the relationship between the intercepted radiation and the LAI, for bread (open symbols) and durum wheat (closed symbols) d). Error bars, when longer than the symbol, stand for the standard deviation of the means.

3. Results

3.1 Leaf area, weight and interception

Along the wide range of experiments bread wheat generally produced a higher number of organs (*v*.g. tillers, leaves, grains) than the durum wheat. In the case of leaves bread wheat produced a larger Leaf Area Index (LAI) and had more leaf weight per m^{-2}, than durum wheat, and the difference grew with the availability of resources (Fig. 1). The leaf N concentration, which was higher in the poor yielding conditions, was relatively higher for the bread wheat on those conditions while it tended to be higher for durum wheat when the environment was higher yielding (Fig. 1c). Comparing the relative capacity of their LAIs to intercept radiation, both wheats presented similar relationships, which was linear at low LAI values and tended to approach the 100% of interception. However, a closer inspection of the data shows that bread wheat presented, relative to durum wheat, a higher significant LAI for the same level of radiation interception, and therefore a higher K for our whole dataset (0.43 vs. 0.54 for durum and bread wheat, respectively). When fitting them independently, the two curves were significantly different ($P < 0.0001$).

3.2 Tillers differential production and growth along the environments between species

Similarly to the differential leaf production between wheat species (Fig. 1a,b), bread wheat produced a higher number of tillers (*c*. 75 stems m^{-2} more) than durum wheat along the whole crop growth, and then the number of spikes was also higher (*c*. 70 spikes m^{-2} more). The difference in spike number between both types of wheat was constant across the wide range of environmental conditions explored, as the slope was not different from 1 (Fig. 2c).

Contrastingly the stem biomass did not follow that general pattern (Fig. 2b), meanwhile leaf biomass in SE was in most of the cases higher for bread (averaged for all conditions 16% heavier), in the case of tillers its biomass was very similar for both species along all the environmental conditions and in most of their developmental stages, and only slightly higher in the highest yielding conditions (fig. 2b). Regarding the stems N content, was *c*. 8 % higher in bread than in durum wheat, probably as a consequence of the higher surface to volume ratio from bread wheat. Observing the stems growth dynamics along the 3 experimental years important differences in weight were generated, and both wheat species weight reached a similar maximum from which it fell until physiological maturity (Fig. 2e). However, the loss of stem weight after anthesis in durum wheat was more severe than in bread wheat, and the difference increased along the increase of environment potential for stem weight loss, slope = 0.66 (Fig. 3f).

3.3 Root length differences at anthesis

Root development along the exp. 2 and 3 presented important differences in root weight and length density, both variables where highly correlated ($R^2 \approx 0.9$) and therefore both variables yielded similar results, unless for the 0-25 cm layer analysis where I incorporated the heavy crown roots (data not shown). Wheat plants in the drier exp. 2 produced a higher root length and weight from under 25 cm deep up until the deepest analyzed layer of 1m, in contrast with the exp. 3 with frequent rains along SE, in which a higher number of roots in the 0 to 25 cm layer was produced (Fig. 3a,b). Comparing the bread *vs*. durum performance for the 0 to 25 cm layer, durum wheat presented very little variation in root production in average along the treatments, while oppositely bread wheat steadily increased the amount of roots in that layer.

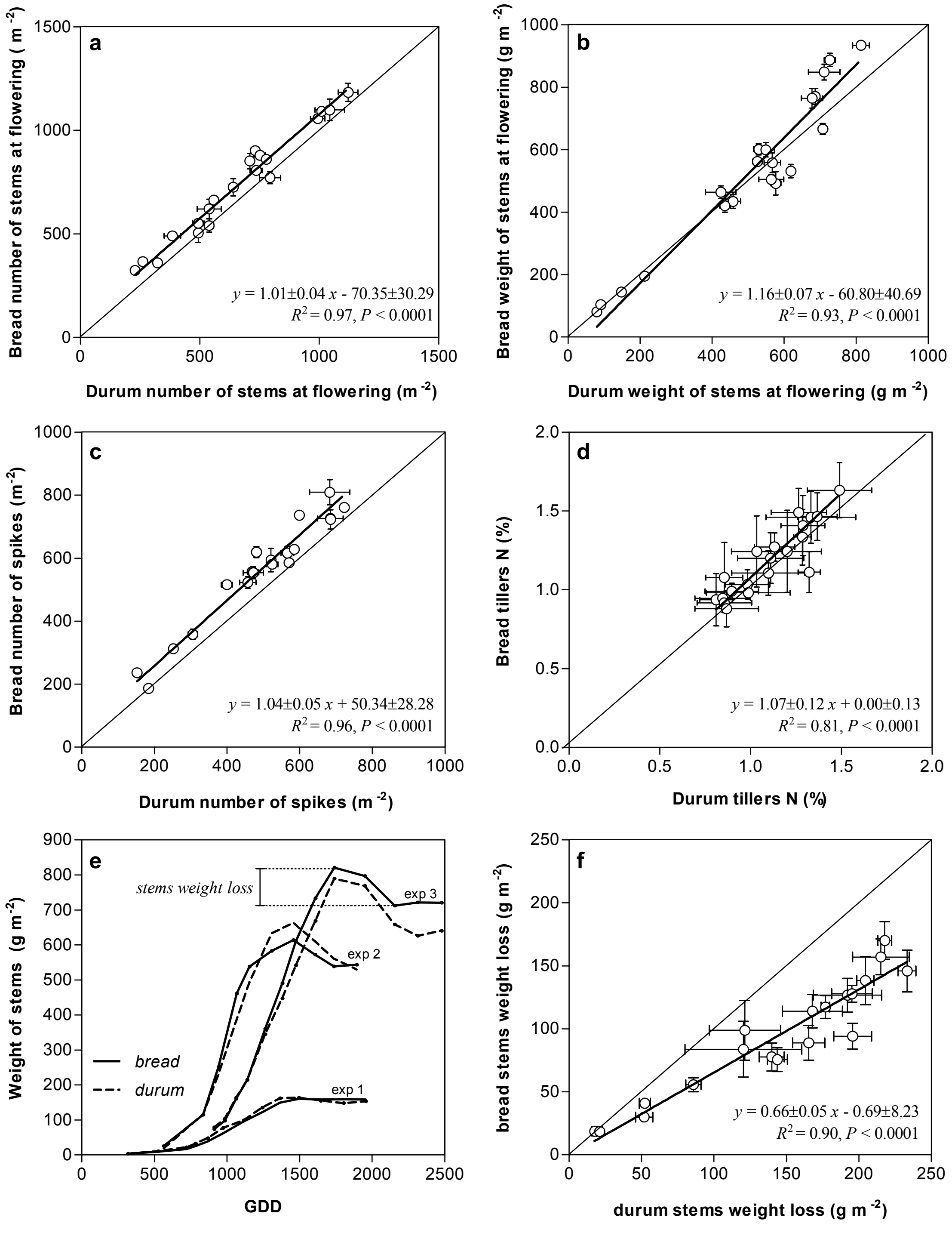

Figure 2. Pairwise comparisons between bread and durum wheat with data from the different experiments carried out in NE Spain for the stem number at anthesis a) for the average weight of stems at anthesis b) the number of fertile spikes c) the stems N concentration d) and de tillers weight loss along post-anthesis f), regressions are shown for the data (thick lines), the 1:1 ratio (thin lines). Dynamics for the stem weight along the crop cycle, bread (plain line) and durum (doted line) e). Error bars, when are longer than the symbol stand for the standard deviation of the means.

Additionally, in the other 25-100 cm deeper layers durum wheat produced more roots in the drier exp. 2, and oppositely bread wheat produced more roots in the wetter exp. 3, along all the analyzed treatments (Fig. 3a,b,c). Nonetheless, a differential pattern in response to the treatments was found (Fig. 3d) which was repeated in the two experimental years: taking into account the two extreme conditions (the irrigation_N200 treatment relative to the rainfed_0), in both experimental years, bread wheat increased the root production respect to durum for the layers 0 to 25 cm and 75 to 100 cm when irrigated and fertilized, while oppositely durum tended to generate a higher proportion of roots than bread wheat, in two layers from 25 to 75 cm deep. And the opposite situation, near to specular, was produced for the rainfed_N0 conditions. That means that durum wheat responded to drought by producing roots more deeply than bread wheat, while bread responded to the increase of environment potential by increasing the amount of roots in the upper layer (Fig. 3d).

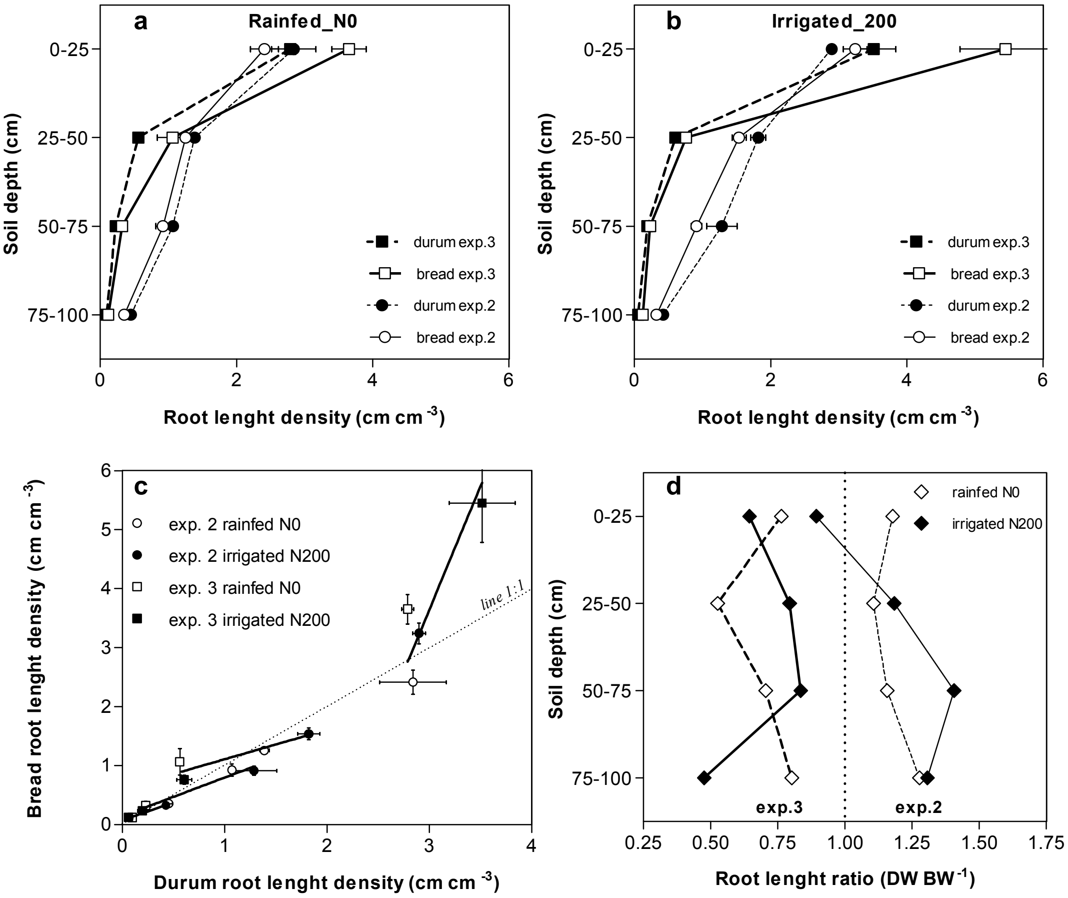

Figure 3. Relationships between the root length density and soil depth for the rainfed a) and the irrigated b) conditions for durum (closed symbols), and bread wheat (open symbols); and for the root length density ratio (durum divided by bread wheat) and soil depth by irrigation treatment, rainfed_N0 (open symbols) and irrigated_N200 (closed symbols), from wheat plots grown side by side though a wide range of conditions in different field experiments under contrasting water and N availability carried out through two growing seasons in NE Spain. In addition, pairwise comparisons between durum and bread wheat for the same experimental data along the treatments and the two experimental years c). Error bars, when longer than the symbol stand for the standard error of the means.

Studying the distribution of the root length density against the root diameter (Fig. 4), most of the roots presented diameters between 0.1 to 0.4 mm and between these diameters in the rainfed treatments from exp. 2 most of the differences between the treatments or species occurred from 0.1 to 0.2 mm of diameter. However, in the irrigated_N200, for exp.2 and 3, the distribution was slightly displaced to higher diameters (Fig. 5b,d) mainly for the upper layers, since the deepest layers look similar between treatments for exp.2, which could be a consequence of the limited irrigation for a particularly dry season, not reaching the deepest layers. Regarding the exp. 3, which presented important rains, it is remarkable the important differences in root length density between bread and durum wheat, particularly in the upper layer for the irrigated and fertilized treatment.

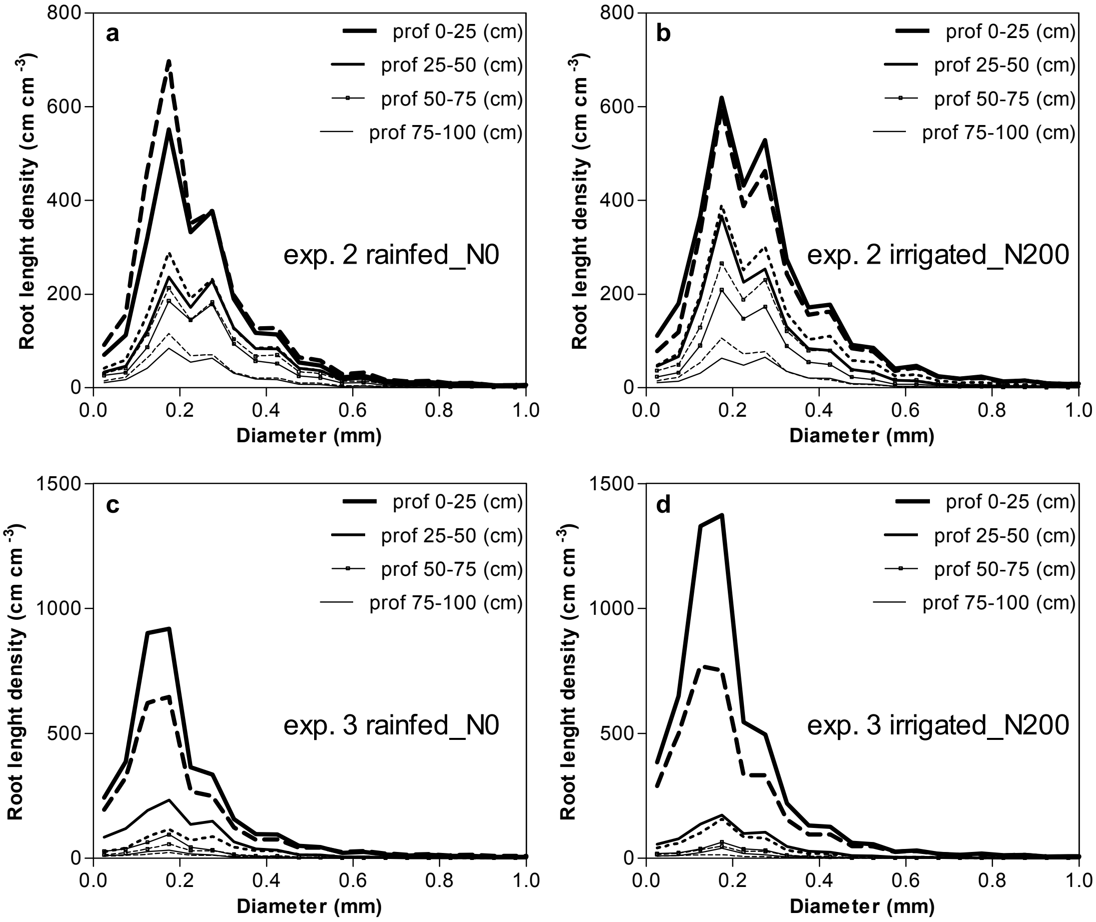

Figure 4. Distribution the root length density by root diameter for the exp. 2 for the rainfed-N0 treatments a), the exp. 2 for the irrigated_N200 treatments b), the exp. 3 for the rainfed_N0 treatments c) and the exp.3 for the irrigated_N200 treatments, for wheat cultivars of bread (plain lines) and durum wheat (dashed lines) grown side by side in NE Spain.

4. Discussion

The geographical pattern of land allocation from the wheat species (Chapter I) could suggest that durum wheat have some yield advantages in the marginal conditions while bread wheat have a higher yield potential. In that line, in our study durum wheat presented some attributes that could potentially alleviate stress in some particular conditions, *i.e.* for water and temperature stresses; durum presented relative earliness in biomass generation until jointing, a higher remobilization of the stem reserves, a lower affectation of grain size in the particularly warm conditions of exp. 2 (Chapter III), a lower leaf area and a superior root exploration of the deeper layers for water; which could be an adaptation to the dry Mediterranean conditions where durum has been traditionally cultivated. In fact, Moragues *et al.*, (2006) found a differential pattern of adaptation to the environments along the Mediterranean distribution of durum wheat, while durum germplasm carrying stress resistant genes were used in bread wheat breeding for the drier areas of Australia (Marshall,1987).

Nonetheless, in most of conditions bread wheat cultivars ended the season producing similar amounts of biomass across a wide range off yielding conditions (chapter III) and therefore the general assumptions commonly accepted by farmers and the literature do not fount support on the relative performance of both wheat species in biomass production either. Bread wheat in comparison to durum wheat tended to generate more organs (tillers, leaves, spikes and grains), commonly of smaller individual weight than durum in most of the environments, in agreement with data of the few available comparisons side by side (*v. g.* López-castañeda and Richards, 1994; Zubaidi *et al.*, 1999; Reynolds *et al.*, 2004). These differences were particularly important in the poor yielding conditions while in proportion diminished with the increase of the environment potential but oppositely the case of roots, was the other way around, in the water prone conditions of exp. 2 durum generated more roots than bread wheat, unless in the top soil layer, while under the big rains from exp. 3 bread in general produced more root biomass and length. Those differences in the allometry of the cultivars are probably the consequence from the expression of D-genome; the hexaploid bread wheat derivates from the cross between a tetraploid wheat like durum and the wild diploid *T. tauschii* Coss (Chapter I), which commonly produces numerous tillers, thin stems, small and narrow leaves, and small grains (Ehdaie and Waines, 2013); that additional ploidy level confers to bread wheat a greater adaptability and numerous loci for constrain resistance have been found on it (Mujeeb-Kazi and Hettel, 1995); however, the physiological effects from those changes in yield are commonly not fully understood.

The higher production of leaves resulted in a higher LAI for bread wheat, despite those differences were compensated by durum with a superior light attenuation coefficient K, and since the specific leaf weight was similar (data not shown). This suggests that consistent differences in leaf angle or size (Fischer, 2001) may exist between the species, those differences could be the cause of the relative earliness in biomass production, before jointing, of durum (Chapter III), which is in agreement with the longer coleoptiles for durum wheat found by Trethowan *et al.*, (2001), while the lower LAI could be an adaptation to water prone conditions (Araus *et al.*, 2002).

The higher bread wheat production of stems and spikes m^{-2}, highly numerically important in the poor yielding conditions, which has been already described in the few papers available (*vg*. López-castañeda and Richards, 1994; Zubaidi *et al*. 1999), produced a gap in the production of grains m^{-2}, producing sink-strength differences after anthesis on those particular conditions, as explained in further detail in Chapter IV. In contrast, in the high yielding conditions the gap of in organs generated, become much less important, and the difference in grains and tillers tended to be reduced. In addition, as postulated by Donald (1968), under high yielding conditions the superior generation of tiller, leaves and root biomass from bread wheat could produce a greater competition between organs, decreasing the relative sink of bread; experimentally the restricted tillering for bread wheat have reported to be an advantage in the high yielding conditions (Duggan *et al*., 2005; Mitchell *et al*., 2012). In addition, the relative higher tiller weight loss in post-anthesis for durum wheat could go in that line since only become relatively important in the most alleviated situations, and related with the singh-strengh size, higher for durum in that situations (Chapter IV); and rather than be a positive factor for the drought prone conditions could be a factor contributing to the relative durum wheat yield potential.

Regarding the differences in root production, our results, in which the larger durum grains produced a greater exploration of the deepest soil layers under stress, will confirm the results found by Mac Key (2005), and for (Grando and Cecarelly, 1995) relating a higher amount of adventitious roots and deeper exploration with grain and coleoptile bigger sizes for the tetraploid durums. In addition, regarding the roots distribution in diameter, our results differed from those from Zubaidi *et al*. (1999) who found them thinner for bread. In our experiments, the distribution in diameter along the treatments was similar for both species or smaller for durum under the rainfed_N0 treatment, in particular for the exp. 2 with lower rains. Furthermore, since the relative bread-durum root length and biomass generation was cross-over with the resources availability, the particular results found for Zubaidi *et al*. (1999) and Hurd (1964) in which durum presented less root production, could be a particular case of that interaction. Furthermore, Zubaidi *et al*. (1999) only studied the soil layer until 60cm deep, which based on our study relative root production pattern until 1m deep, could affect the results.

In conclusion, despite the fact that durum wheat cultivars analyzed presented certain characters favourable for the restricted water environments, no advantages in biomass have been found for that species in the poor yielding conditions, and therefore the durum relative sink-strength limitation under stress may limit the effect of those advantageous traits.

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Chapter VI: Bread and durum wheat relative nitrogen, water and radiation capture and use efficiency

Abstract

Differences in yield found along the environmental range between bread and durum wheat were also related to differences in radiation, water and nitrogen use efficiencies: under low-yielding conditions bread wheat was consistently more efficient than durum wheat and under high-yielding conditions durum wheat tended to be more efficient. Regarding the radiation use efficiency (RUE) the differences were given by differences in post-anthesis biomass, likely because differences in both, interception and efficiency; while for the N use efficiency (NUE) were related to differences in N uptake rather than in N utilization and therefore to differences in capture rather than in partition. In addition, cultivars under fertilization maintained relative high contains of grain N%, which confirm the possibility to cultivate durum wheat under good yielding conditions, as the relative grain N contain between both species was not related, under those conditions, to the potential yield of the environments.

Keywords: Radiation use efficiency, water use efficiency, nitrogen use efficiency, N uptake efficiency, N utilization efficiency, N grain concentration

1. Introduction

As argued in Chapter I, comparing bread and durum wheat cultivars is relevant in terms of productivity and the physiological bases behind their differences. In this chapter the focus is in the capture and use efficiency of resources. Irrigation and fertilization, when possible, are expensive or restricted due to environmental protection. Thus, water and N are commonly applied in limited quantities, taking relevance its efficiency in economical and ecological terms. Searching for improvements in use efficiency must be taken cautiously as in some cases it may result in (or be the result of) reduction in the capture of resources. Thus there is not always a positive relationship between resource use efficiency and yield, as in many conditions yield is better related to the genotypic capacity to capture more resources (Blum, 2005). However, positive associations between resource use efficiency and yield were reported when the resource in question was water (French and Schultz, 1984; Angus and Herwaarden, 2001; Zhang *et al*., 1998), nitrogen (Ortiz-Monasterio *et al*., 1997; Raun and Johnson, 1999) or radiation (Calderini *et al*., 1997; Miralles and Slafer 1997; Reynolds *et al*., 2000). In addition there are synergies and interactions between the use of the different resources. For instance, a higher leaf area index (LAI) can increase simultaneously radiation interception and plant transpiration increasing water consumption but reducing water use efficiency. Post-anthesis differences in sink-strenght have been observed to impact on RUE in that period (Calderini *et al*., 1997, Reynolds *et al*., 2005), as a consequence of its regulation of photosynthesis (Wang *et al*., 1998; Calderini *et al*., 2006).

As reviewed in chapter I but further extended here, Zhang and Oweis (1999), found durum wheat more efficient than bread wheat in the water use, despite the contrastingly smaller response of durum to irrigation. In addition, they found bread wheat negatively correlated with vapour pressure deficit during grain filing while durum wheat was not, presumably explaining the greater durum wheat drought resistance in comparison with bread wheat. About the nitrogen economy, Dhugga and Waines (1989) reported differences in the nitrate uptake rate for durum and bread wheat; while other authors, despite few exceptions when N was limited, found bread wheat to be more efficient in N uptake efficiency (NU_pE) relative to durum wheat contributing to NUE (Ehdaie *et al*., 2001; López-Bellido *et al*., 2008); in addition, late fertilizations generated advantages in NUE for bread particularly in post-anthesis explaining a greater post-anthesis dry matter accumulation for bread wheat (Ashraf and Azam, 1998). Meanwhile bread wheat, because of a presumed higher productivity, could uptake more N and was more efficient in its use for grain production and contrastingly durum wheat obtained the highest N grain concentration (Geleto *et al*., 1996; López-Bellido *et al*., 2008).

The aim of this chapter was to test whether the capacity for resource capture of these two species of wheat is different and whether differences in resource use efficiency may be relevant in explaining yield differences found in Chapter II. The results were initially expected to shed light on the commonly accepted axiom that durum wheat would be more efficient in the use of resources under stressful conditions and that, oppositely, bread wheat would have higher efficiency in the use of resources at high-yielding conditions.

2. Materials and methods

To achieve the objective of this chapter I further analyzed the side-by-side experiments detailed in Chapter II in conjunction with a meta-analysis with data from the literature papers reporting data on resource use and use efficiency.

2.1 Field experiments

Daily incident radiation was taken from a public Meteorological Station next to the experimental zone, and the amount of intercepted radiation by the crop was calculated weekly as in described in Chapter V. In addition, the Normalized Difference Vegetation Index (NDVI), which relates the difference between near infrared reflectance and red wavelength reflectance with the reflectance of both wavelengths, which is an aproximation of the canopy green biomass and radiation interception, was mesured from weekely readings of the canopy reflectance using a portable spectroradiometer (Greenseeker Hand HeldTM optical sensor unit, model 505; NTech Industries, Inc., Ukiah, CA, USA). The amount of radiation captured by the crop, the accumulated fraction of Intercepted Photosynthetically Active Radiation (ΔfIPAR) was calculated in a daily base, and summed for a given period, from halve of the daily incident radiation (the theoretical fraction absorbed by plants) by the percentage of intercepted radiation in the week. The interception efficiency was calculated as the coefficient for light attenuation (k) as explained in Chapter V. The radiation use efficiency was calculated for the period from jointing to anthesis by dividing the accumulated biomass by the accumulated fIPAR.

To calculate water and nitrogen use efficiency, soil samples were collected prior to sowing and after maturity at four different depths (0-25; 25-50; 50-75 and 75-100 cm) to measure water and nitrogen contents and to calculate their availability. Water content was gravimetrically determined weighing the samples before and after drying the soil samples at 105 ºC for 48 h. N availability was assessed by estimates of soil $N\text{-}NO_3^-$ content with Nitracheck reflectometer methodology (Merckoquant Nitrate strips). Water use (WU) was estimated as the sum of the growing season precipitation plus irrigation plus the growing season change in soil water content for the rooting zone, I considered runoff and drainage to be negligible; water use efficiency (WUE) was calculated as grain yield per unit of crop water use.

After determining dry weight of the different organs, samples were processed and N content was determined by the Kjeldahl method for each of the organs in which dry matter was determined. With the data of N uptake I estimated N use efficiency (NUE), following Moll *et al.* (1982), as grain yield per unit of soil N supply (mineral soil N available at sowing in the top 100 cm, plus fertilisation rate); and its two components, N uptake efficiency (NU_pE), the ratio of total plant N uptake to N supply, and N utilisation efficiency (NU_tE), the ratio of grain yield to total plant N uptake. Literature data from NU_pE higher than 1 was disregarded because of the underestimation of soil N contain.

2.2 Literature data

I further used data from the literature database presented in chapter II, with papers reporting data on capturing or nutrients use efficiency, in addition to yield. Unfortunately, few papers reported data of radiation use or efficiency, with both wheat species grow together, and for this topic I only report our own data in this chapter.

2.3. Data analysis

Data from bread and durum wheat were analysed using regression analyses. In all the analyses when regressing a variable in bread wheat against the same variable in durum wheat both variables were subjected to error, thus I fitted the regressions with Model II (Ludbrook, 2012).

The raw data of variables measured weekly were adjusted for each experimental unit by non-linear regression to a logistic curve against accumulated thermal time (Tb = 0 ◦C), with the NLIN procedure from SAS software (SAS Institute, 2004), all relationships where highly significant ($R^2 > 0.90$; $P < 0.001$).

3. Results

3.1 Nitrogen uptake, grain nitrogen and grain nitrogen concentration

The total amount of N uptake was importantly affected by nitrogen availability and irrigation (Table 1) and the relationship between total nitrogen uptake at maturity was curvilinearly related to yield and was similar between the two species, as well as for data from our experiments and from the literature (Fig. 1a); the relationship was tight for relatively low levels of N-uptake while at higher levels of uptake yield tended to be less related to it (Fig. 1a). Although in general data from both wheat types are overlapped, when compared pairwise, in average bread wheat absorbed more nitrogen in the lower-yielding conditions than durum wheat, while for yielding conditions above the average yield of the whole data set both wheat species tended to uptake in average similar amounts of N (Fig. 1b). In addition the data showed an interaction with the yielding environment similar to the one for yield discussed in detail in Chapter II, and therefore the variation in Nuptake was importantly related to the variation in yield for our experiments ($R^2 = 0.81$; $P < 0.0001$) as well as for the whole dataset combining the experimental data and the data taken from the literature ($R^2 = 0.66$; $P < 0.0001$).

Table 1. Means and significance of the difference for total N uptake, grain N yield, grain N%, NUE, NU_pE and NU_tE measured at maturity along tree experimental years, for two species of wheat (bread and durum wheat), each of the tree levels of irrigation (rainfed, fully irrigated, irrigated before anthesis and after anthesis) and the two nitrogen fertilisation levels (0 or 200 kg ha^{-1} of N fertilizer)

		Bread	Durum	Rainfed	Irrigated	Irrigated pre-anthesis	Irrigated post- anthesis	N0	N200
Exp. 1	NUE	11.16a	8.76b	4.63b	15.29a	-	-	12.63a	7.28b
	NU_pE	0.38a	0.35a	0.21b	0.52a	-	-	0.42a	0.30b
	NU_tE	26.55a	22.48a	20.81b	28.23a	-	-	27.24a	21.79b
	Total N uptake	76.95a	68.54a	46.89b	98.60a	-	-	58.91b	86.58a
	Grain N yield	54.97a	47.34a	29.92b	72.40a	-	-	42.87b	59.44a
	Grain N %	2.73a	3.03a	3.07a	2.69a	-	-	2.73b	3.03a
Exp. 2	NUE	17.86a	16.36a	13.59a	18.35a	18.80a	17.71a	23.27a	10.95b
	NU_pE	0.57a	0.55a	0.47a	0.61a	0.59a	0.58a	0.65a	0.48b
	NU_tE	29.79a	28.20a	27.34a	29.17a	29.58a	29.91a	35.16a	22.84b
	Total N uptake	195.67a	189.99a	158.75b	233.42a	213.11a	166.07b	147.20b	238.47a
	Grain N yield	128.81a	131.63a	100.73b	163.28a	143.86a	113.01b	109.78b	150.66a
	Grain N %	2.43b	2.53a	2.45ab	2.52ab	2.62a	2.33b	2.15b	2.81a
Exp. 3	NUE	24.97a	23.91a	24.50ab	26.87a	25.94ab	20.46b	26.00a	22.88b
	NU_pE	0.72a	0.71b	0.74a	0.75a	0.74a	0.63a	0.68b	0.75a
	NU_tE	34.51a	33.56a	33.23b	35.88a	34.68ab	32.35b	37.86a	30.22b
	Total N uptake	183.46a	194.57a	192.76a	195.06a	193.20a	175.04a	128.20b	249.83a
	Grain N yield	126.36b	138.61a	132.99ab	139.06a	138.15a	119.72b	92.77b	172.19a
	Grain N %	2.04b	2.18a	2.15ab	2.00b	2.09ab	2.20a	1.91b	2.31a

NUE, Nitrogen use efficiency; NU_pE, Nitrogen uptake efficiency and NU_tE, Nitrogen utilisation efficiency. The different letters means significance under 0.05 with the Duncan statistic.

Grain N yield was closely related to grain yield presenting a very similar relationship between the two wheat species overall the dataset, with no differences either between the data from our experimental conditions or from the literature (Fig. 1c). Thus comparing that variable pairwise, in the same field conditions, bread wheat tended to have higher N yields than durum wheat in the poorer conditions whilst in the high yielding condition this advantage was lost (Fig. 1d).

Grain N concentration was rather conservative (compared to N uptake and N yield, which varied several folds), not being as strongly affected by the environment as it was affected yield (Fig. 1e). However, with the increase of yield potential variation in N concentration narrowed in our datased stabilizing around 2%, and tended to be slightly higher in durum than in bread wheat along the environmental range (Fig. 1f) and the tree experimental years (Table 1). Additionally irrigation decreased the concentration of N in the grain, particularly in exp. 1 which was very dry, and significantly increased with the fertilization, along all the experimental years.

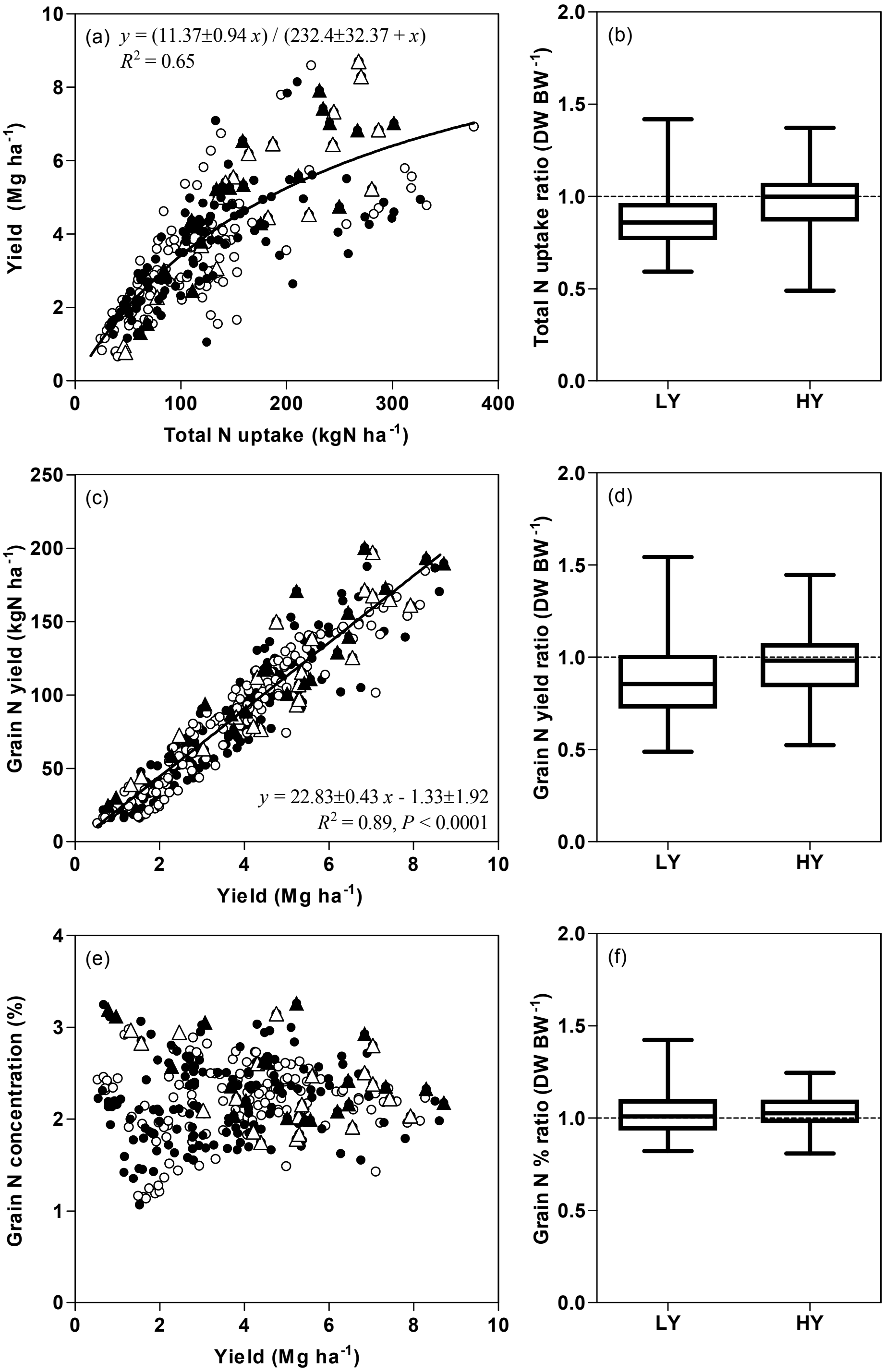

Figure 1. Relationships between yield and total N uptake (a), and between grain N yield (c) or concentration (e) and yield, for bread (open symbols) and durum wheat (closed symbols). Data taken from the literature (circles) or from our experiments, in NE Spain (triangles). Plain lines and equations stand for the regression analysis of all the data together and each relationship is accompanied with a boxplot of the ratio of each N-economy traits between durum and bread wheat, after dividing the dataset in two conditions higher- (HY) and lower-yielding (LY) than the overall average yield (b, d and f).

3.2 Water use

Both species behaved very similarly in water use, since no significant differences along our tree experimental years were found (Table 2). Comparing all data together (from our experiments as well as from the literature) most data points feld close to the 1:1 ratio (Fig. 2c), and consequently, neither under low- nor under high-yielding conditions existed clear advantages of any of the wheat species over the other one in using water (Fig. 2d); and in the whole dataset, neither in rainfed nor in irrigated conditions, the fits of the bread and durum wheat relationships differed significantly ($P > 0.05$) and therefore where analyzed together.

Regarding the irrigation treatments it is remarkable, that the relationship between water use and yield for the rainfed conditions was very tight, for our experiments ($R^2 = 0.77$; $P < 0.0001$), presenting a higher slope in comparison with the relationship for the irrigated conditions; meaning a higher response and efficiency to water availability for the rainfed conditions; a similar response was found for the literature data despite the smaller R^2 (Fig. 2a,b). The linear regressions of the rainfed and the irrigated treatments datasets, in our experiments and the literature where statistically different ($P < 0.001$) (Fig. 2a,b). The remarkably high range of variation from yield *vs.* WU in the rainfed conditions of our dataset, mainly performed in Mediterranean environments, highlights the importance of many other factors in determining the WU and the WUE, *e.g.* nitrogen fertilized treatments presented important water x nitrogen interactions (Table 2) which made in the three experimental years to increase WU and the WUE.

Table 2. Means and significance of the difference of WU and WUE measured at crop maturity along tree experimental years, for two species of wheat (bread and durum wheat), each of the tree levels of irrigation (rainfed, fully irrigated, irrigated before anthesis and after anthesis) and the two nitrogen fertilisation levels (0 or 200 kg ha^{-1} of N fertilizer)

		Bread	Durum	Rainfed	Irrigated	Irrigated pre-anthesis	Irrigated post- anthesis	N0	N200
Exp. 1	WU	260.54a	257.25a	183.63b	334.17a	-	-	256.20a	261.59a
	WUE	7.70a	5.79a	5.37a	8.12a	-	-	6.31a	7.18a
Exp. 2	WU	279.06a	283.67a	222.89c	345.36a	322.23b	234.99c	276.28b	286.46a
	WUE	19.42a	18.27a	18.32a	18.61a	17.72a	20.73a	18.71a	18.98a
Exp. 3	WU	470.53a	477.67a	343.62d	593.37a	550.24b	409.18c	459.55b	488.64a
	WUE	13.24a	13.68a	17.45a	11.51b	11.78b	13.11b	11.11b	15.82a

WU, Water use; WUE, Water use efficiency. The different letters means significance under 0.05 with the Duncan statistic.

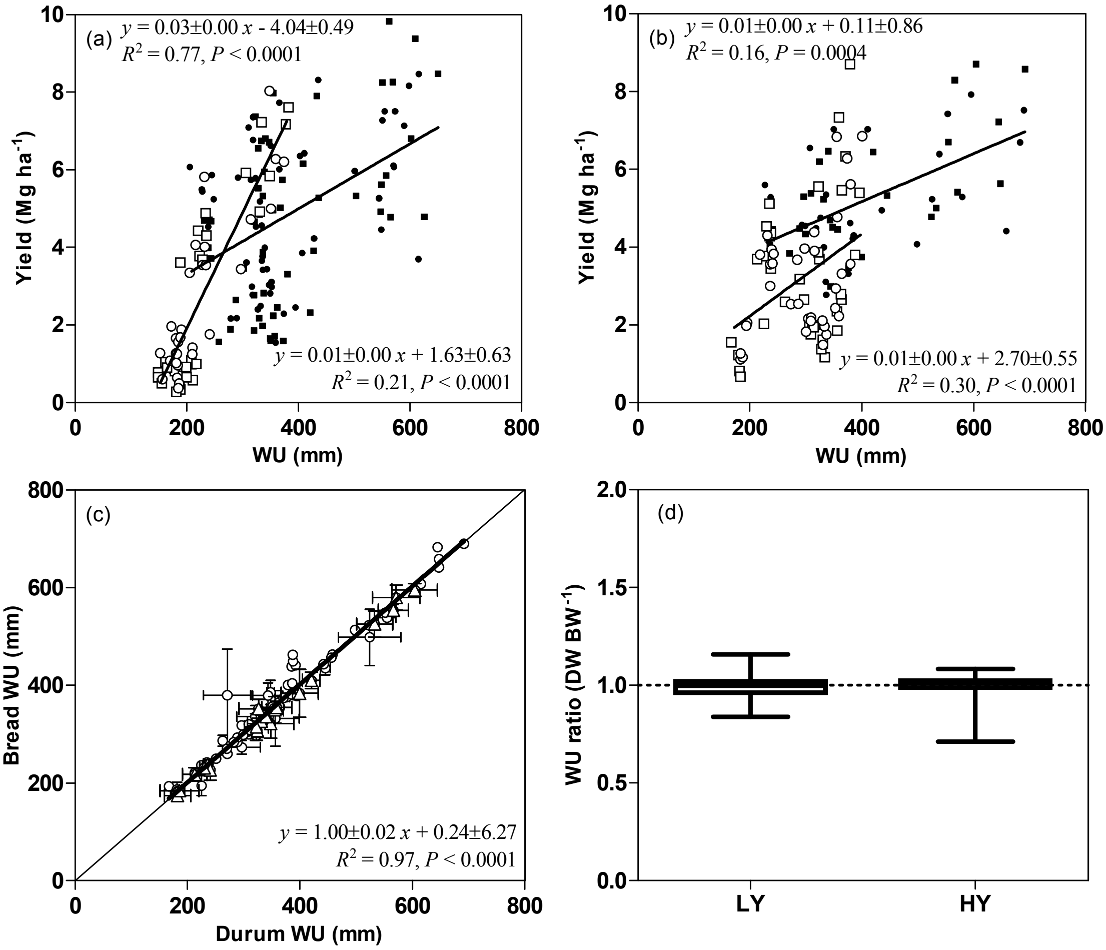

Figure 2. Relationships between yield and water use (WU), for the tree experimental years in Lleida and in the literature dataset respectively (a and b); and pairwise comparisons between durum and bread wheat from cultivars sown in the same environmental conditions for water use (WU) (c), the relationship is accompanied with a boxplot of the ratio for WU between durum and bread wheat, after dividing the dataset in two conditions of yield being higher- (HY) and lower-yielding (LY) than the overall average yield (d). In the two upper figures, data for the rainfed treatments (open symbols), irrigated (closed symbols), bread wheat (circles) and durum wheat (squares); the regression lines either in the rainfed or in the irrigated conditions for the twoo species were not different and the line is for both datasets together (a and b). In the lower figures, data for experiments carried out in NE Spain (triangles) and collected from published studies (circles); the regression line for data from the literature review or our experiments were not different and the line is for both datasets together (c). The thin lines stand for the 1:1 ratio (c). The thick lines and the equations stand for the regression analysis.

3.3 Light interception and radiation use.

The fraction of intercepted radiation calculated with the ceptometer was very similar for both species along the 3 experimental years (Fig. 3a); and both species responded to the availability of resources by intercepting more radiation, producing an important range of intercepted radiation along the yielding environments, before (from jointing to anthesis) and after anthesis (*c*. 30-470 MJ m^{-2} and *c*. 40-345 MJ m^{-2}, respectively). Therefore, considering most of the crop cycle growth period, from jointing to maturity *c*. 70-700 MJ m^{-2}; both species presented a very similar relationship of the cumulative intercepted radiation and yield (Fig. 3c).

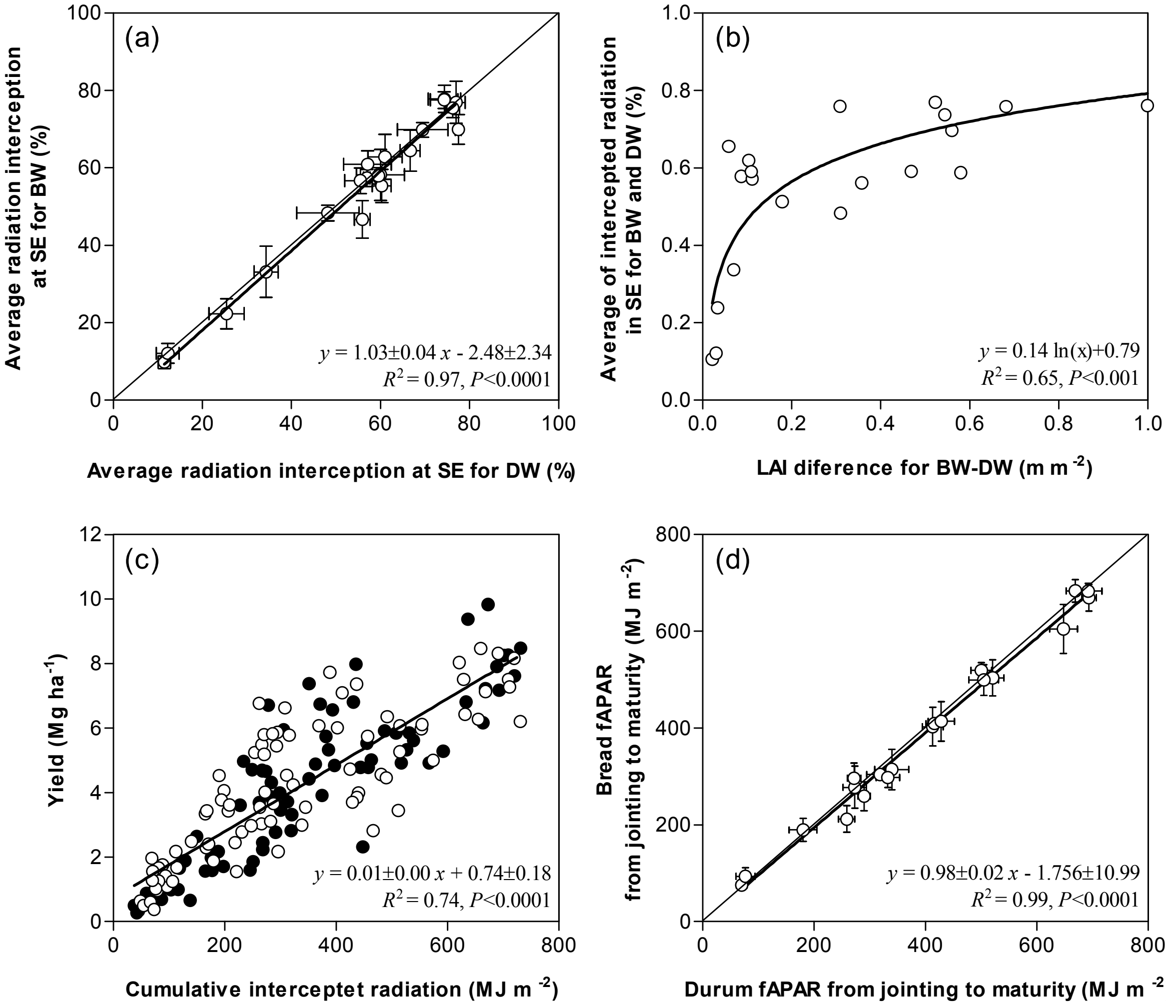

Figure 3. Pairwise comparisons between bread and durum wheat with data from the different experiments carried out in NE Spain for the average percentage of intercepted radiation in stem elongation (SE) (a) and for the accumulated intercepted radiation from jointing to maturity (d); and the relationship between the average intercepted radiation and the difference (bread wheat-durum wheat) in LAI (Leaf Area Index) for each environment at SE (b), and between the cumulative intercepted radiation (from jointing to maturity) and yield (c).

Regarding the efficiency in light interception, durum wheat presented a higher attenuation coefficient (K) than the bread wheat (Chapter V) and therefore a higher interception of radiation for unit of LAI, which bread wheat compensated along the 3 experimental years producing a higher LAI (Fig. 3b). Finally, as a consequence of bread wheat producing more leaf area and biomass than durum wheat the intercepted radiation for both species along the environments was rather similar both before (from jointing to anthesis) and after anthesis (Table 3). Nonetheless, in the dry exp. 1 bread wheat in average intercepted a 6% more radiation than durum wheat and inversely in the exp. 2 and exp. 3 durum wheat tended to intercept more than bread wheat (Table 3).

Table 3. Means and significance of the difference for fAPAR and RUE from jointing to maturity along tree experimental years, for two species of wheat (bread and durum wheat), each of the tree levels of irrigation (rainfed, fully irrigated, irrigated before anthesis and after anthesis) and the two levels of nitrogen fertilisation (o or 200 kg ha^{-1} of N fertilizer)

		Bread	Durum	Rainfed	Irrigated	Irrigated pre-anthesis	Irrigated post- anthesis	N0	N200
Exp. 1	fAPAR	158,96a	150,02a	78.87b	230.12a	-	-	128.68b	180.30a
	RUE	2.70a	2.22b	2.53a	2.39a	-	-	2.53a	2.39a
Exp. 2	fAPAR	311.99a	330.07a	275.30a	361.96a	367.50a	279.36a	287.02b	355.03a
	RUE	3.53a	3.35a	3.22a	3.57a	3.46a	3.51a	3.59a	3.29a
Exp. 3	fAPAR	572.08a	582.36a	596.90a	594.89a	593.17a	523.92b	486.37b	668.08a
	RUE	2.40a	2.29a	2.25b	2.43a	2.41a	2.30ab	2.15b	2.54a

fAPAR, Fraction of the accumulated photosynthetically active radiation; RUE, Radiation use efficiency. The different letters means significance under 0.05 with the Duncan statistic.

3.4 Nitrogen, water and radiation use efficiencies

Efficiencies of durum and bread wheat in the use of the N presented an interaction with the yielding environment. Alike what was observed for yield in Chapter II, bread wheat tended to be more efficient than durum wheat under low-yielding conditions and *vice-versa* (Fig. 4). Dividing NUE into its components, N uptake (NU_pE) and N utilization (NU_tE) efficiencies, showed that the differential behaviour of bread and durum wheat in terms of NUE was mainly due to the differences in NU_pE (Fig. 4d), but also to differences in NU_tE (Fig. 4f).

Regarding the water economy, in the exp. 1 and 2, (dry experiments) the full irrigated treatments increased WUE, contrasting with the exp. 3 (wet) in which the rainfed conditions presented the highest efficiency. Interestingly, despite the differences where not statistically significant, the post-anthesis irrigation presented a higher WUE than the full irrigation or the pre-anthesis irrigation treatments. The differences on the relative performance for both species were related partially to the fact that bread wheat was more productive under low-yielding conditions, while durum wheat tended to produce more under high-yielding conditions at the same time that both species used similar amounts of water (Fig. 5a,b); despite that, the regression with data from our experiments did not differ significantly from the 1:1 line, as a consequence of the higher response of bread wheat to post-anthesis irrigations than that of durum wheat; contrasting with the literature data regression which crossed the 1:1 line *c*. 5 kg (ha mm^{-1}).

The radiation use efficiency (RUE) considering the period from jointing to maturity was slightly higher in bread wheat than in durum wheat in average for the 3 experimental years (Table 3; Fig. 5c). However, only in the first experimental year, with the poorest experimental conditions, the differences were statistically significant. After dividing the crop cycle in pre and post anthesis as a consequence from the crossover interaction in post-anthesis for the relative biomass between both species, even thought the interception of

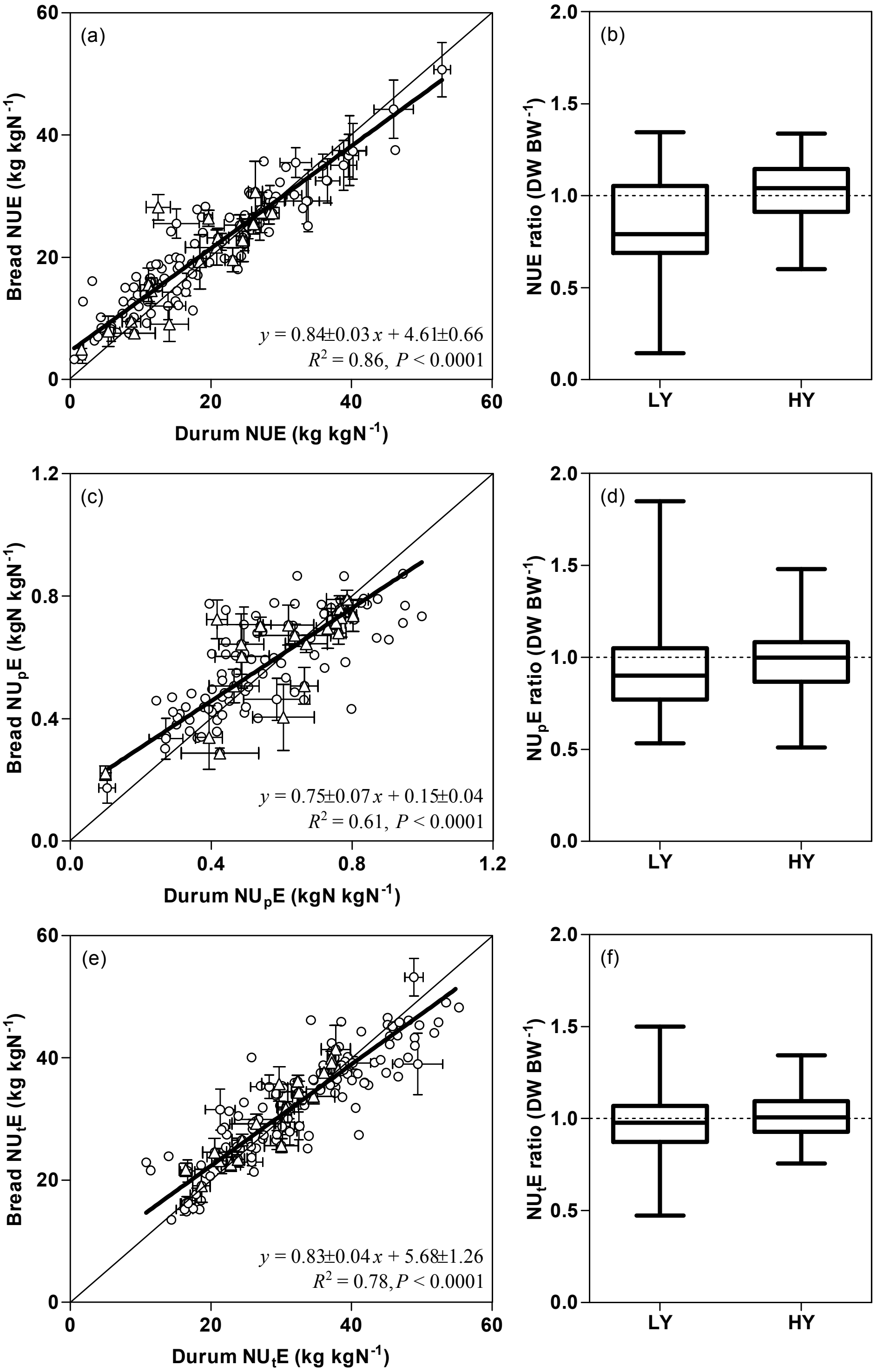

Figure 4. Pairwise comparisons between durum and bread wheat from cultivars sown in the same environmental conditions for Nitrogen use efficiency (NUE) (a), Nitrogen uptake efficiency (NpUE) (c), and Nitrogen utilization efficiency (NtUE) (e). Data for experiments carried out in NE Spain (triangles), or collected from published studies (circles). The plain thick lines and equations stand for the regression analysis of all data together. The plain thin lines stand for the 1:1 ratio. Each relationship is accompanied with a boxplot of the ratio for each N efficiency trait between durum and bread wheat, after dividing the dataset into conditions higher- (HY) and lower-yielding (LY) than the overall average yield (b, d and f).

radiation (measured with the ceptometer) was fairly similar, the relative (RUE) in post-anthesis for both cultivars also presented a slope smaller than 1 (slope = 0.63±0.11); and contrastingly before anthesis, despite slightly higher in average, the relative RUE for both species was not different to the 1:1 line ($P > 0.05$). Nonetheless, in post-anthesis, despite the interception of radiation measured with the ceptometer was rather similar, the NDVI lecture presented a significative interaction with the environment ($P > 0.05$) and the bread *vs*. durum relationship was different from the 1:1 line, (slope = 0.89±0.04).

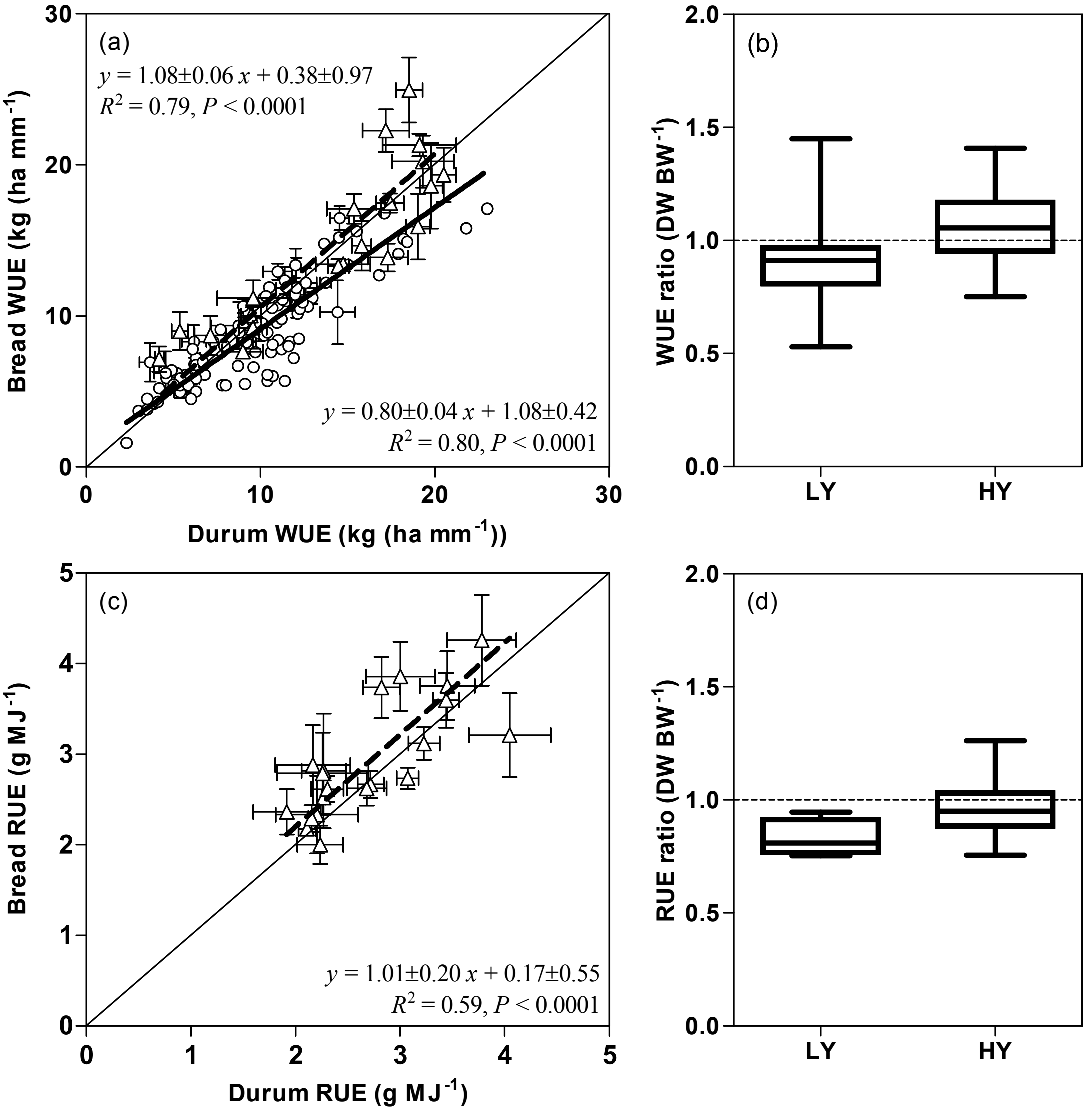

Figure 5. Pairwise comparisons between durum and bread wheat from cultivars sown in the same environmental conditions for water use efficiency (WUE) (a) and radiation use efficiency (RUE) (c). Data for experiments carried out in NE Spain (triangles) and collected from published studies (circles) only for WUE. The thick lines and the equations stand for the regression analysis; there is a regression line for the literature data (plain, b) or our experimental data (dashed, b and c). The thin lines stand for the 1:1 ratio (a and c). Each relationship is accompanied with a boxplot of the ratio for each water and radiation economy trait between durum and bread wheat, after dividing the dataset in two conditions of yield being higher- (HY) and lower-yielding (LY) than the overall average yield (b and d).

4. Discussion

As discussed in chapter II, the assumption that durum wheat is more efficient in the use of resources under the stressful Mediterranean conditions, extensively assumed (*e.g*. Zhang and Oweis, 1999; Monneveux *et al*., 2012,) did not find support in the relative capacities for capturing and using resources of bread and durum wheat data analyzed in this chapter. Instead bread wheat was found, more efficient in the use of some resources, particularly under the harsh conditions from the exp. 1, and therefore in our experiments that species presented a higher NUE, being involved both components NU_pE and NU_tE; a higher WUE, despite differences where not statistically significant; and a higher RUE, particularly again in the first experiment. Therefore, oppositely to the general hypothesis of durum wheat to be more efficient under the poor yielding conditions, I found that in most of the comparisons, either in our experiment or in the literature analysed, bread wheat was more efficient and that those differences where diluted and became cross over under the highest yielding conditions (Figs. 4 and 5).

4.1. Nitrogen economy

In the present database, bread wheat NUE was relatively higher in most of comparisons than in durum, and additionally NU_pE was found to be the component which contributed more to NUE variation, along the environment potential (Fig. 4), which is in agreement with some other previous reports (*e.g*. Ehdaie *et al*., 2001; Ladha *et al*., 2005; López-Bellido *et al*., 2008). Some of the N economy variables: Total N uptake, Grain N yield, and the related efficiencies NUE and NUpE were clearly following the yield variation pattern and therefore generated crossover relationships for bread and durum wheat (Fig. 1 and 4) when compared pairwise. Unlike in the papers by Edhaie *et al*. (1999) and López-Bellido *et al*., (2008), I did not find that NUE was higher for durum under limiting N conditions, and in line with the yield cross-over pattern, I found that only under the irrigated and fertilized treatments the efficiency was similar or higher for durum. Contrastingly the more conservative N economy variables in response to changes in yield potential of the environment were grain N concentration and the NU_tE, for our whole dataset and each species independently (data not shown), as a consequence little differences for those variables were found between both species along the environmental variation in yield potential. Nonetheless, in most of the comparisons durum exhibit a slightly higher grain N concentration, as it is frequently shown in the literature (*e.g*. Geleto *et al*., 1996; Liu *et al*., 1996; López-Bellido *et al*., 2008) and the species relationship for NU_tE presented a slope smaller than 1 which was mainly determined in our experiments by the harvest index ($R^2 = 0.6$). Additionally it is important to remark that N fertilization was able to maintain high nitrogen levels in both bread and durum at high yields.

4.2. Water economy

The relative performance of bread and durum wheat WUE was related in part to differences in yield (Fig. 5), the relative species WUE when ordered with the average yield was following a crossover pattern which made bread wheat more efficient under the lower yielding conditions and oppositely durum to be more efficient for the high yielding conditions, despite WU was rather similar for both wheat species. In contrast with Zhang and Oweis (1999), based in our experimental data, durum wheat do not present higher WUE in most of the cases. However, a significant advantage in WUE ($P = 0.007$) for bread wheat was found when irrigation was in post-anthesis, being the more efficient of all treatments in the exp. 2, a moderately dry year, this could be linked to the greater bread wheat plasticity to late resource availability as reported by Ashraf and Azam (1998) for NUE. Nonetheless, under the harsh Mediterranean conditions heavy rains until maturity (as the post-anthesis irrigation treatment) are rather uncommon; and therefore not considering that particular irrigation, the line comparing pairwise the species for WUE crossed the 1:1 line, in our experiments and in the literature, at rather low efficiencies, which could be explained by the relatively lower LAI, deeper rooting and early development from durum wheat.

4.3. Radiation balance

Again, the relative performance between both wheat species in RUE (from jointing to maturity) was following the cross over interaction in yield, and the relative change in RUE *vs*. the yielding potential was crossover (Fig. 5d), furthermore the relative species variation in RUE expressed as the ratio (DW BW^{-1}) in each pairwise comparison was importantly related to the variation in yield ($R^2 = 0.63$; $P < 0.0001$), this was not clearly seen in the Fig. 5c, as a consequence of the high use of radiation from exp. 3, decreasing the RUE in that year meanwhile being the highest RUE found in the exp. 2 (Table 3). Therefore, as the relative radiation use was quite similar between the species (Fig. 3d), the environmental yield potential and the differences in biomass production were the major causes for RUE variation. However, dividing the crop cycle in pre and post-anthesis, only in post-anthesis differences in RUE were found (Fig. 6a and c), in line with the differences in biomass formed in post-anthesis between both species. These results are in agreement with other experiments from the literature where differences in biomass and RUE, as a consequence in sink-strength differences, were only found in post-anthesis between old and modern cultivars (Calderini *et al*., 1997) or near-isogenic lines with different dwarf gene dosage (Miralles and Slafer 1997).

In addition, despite no significant differences in the interception between both species was found with the ceptometer in post-anthesis; and the relative pairwise comparison for that variable was not different from the 1:1 line, considering the NDVI index as a good estimator of the interception, a crossover relationship was found significantly different from the 1:1 line in the post-anthesis period while no differences where found before anthesis (slope = 1.05; $P > 0.05$). As a result, an important part of the variation in the relative NDVI lectures averaged for the post-anthesis period where related to the relative variations in yield performance and no relationship was found in the pre-anthesis period ($R^2 = 0.02$) (Fig. 6b,d). This indicates that differences in post-anthesis biomass, as discussed in Chapter IV, were sink-strenght driven and related to differences of radiation interception. The fact that no significant differences were found in the post-anthesis period with the ceptometer could be a consequence of the difficulty to place manually the sensor over the senescent leaves, being that variable subjected to a greater error than in pre-anthesis, or because the NDVI index integrates other factors related with RUE.

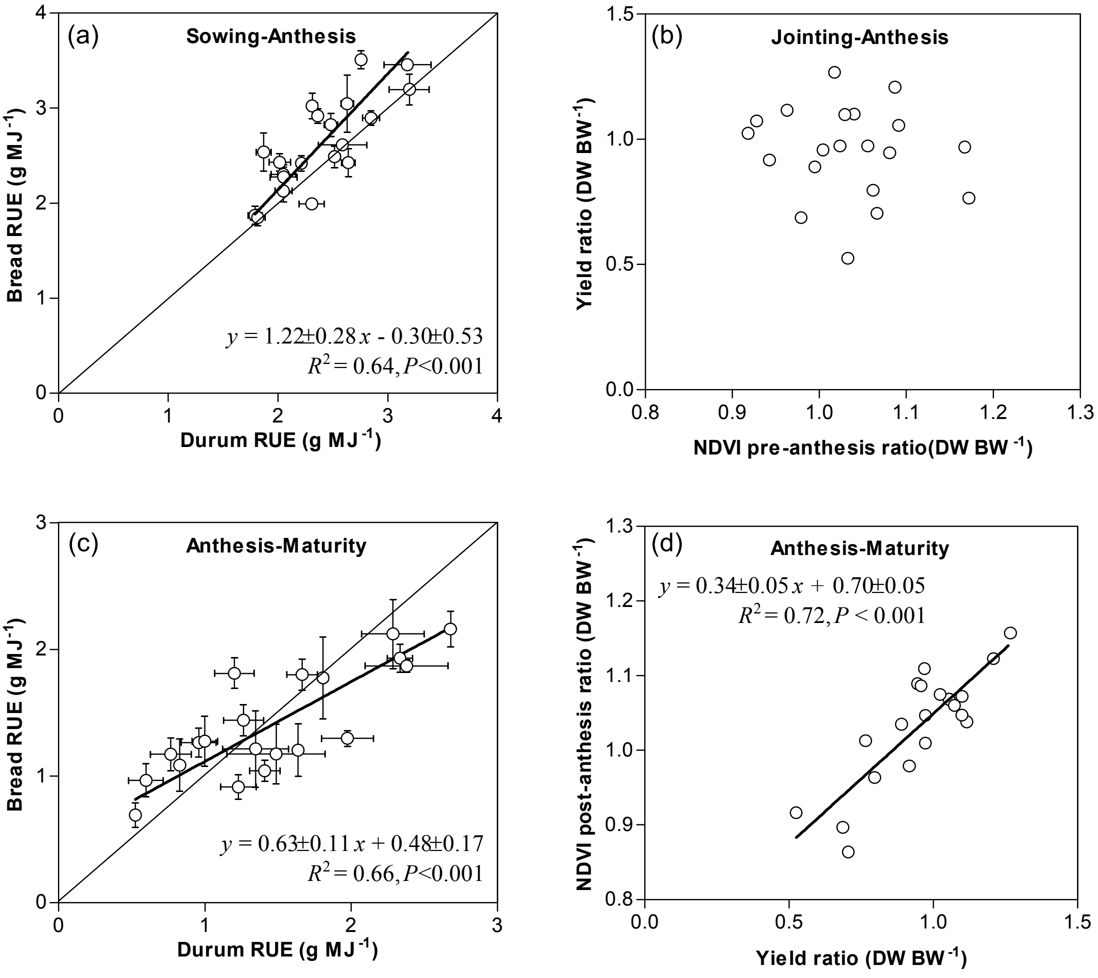

Figure 6. In the left side, pairwise comparisons between bread and durum wheat with data from the different experiments carried out in NE Spain, for the pre-anthesis RUE (Radiation use efficiency) a) and for post-anthesis RUE c). In the right side, relationship between the yield ratio (durum yield divided by bread wheat yield) and the NDVI (normalized difference vegetation index) ratio before anthesis b) and after anthesis d).

The fact that the bread cultivars presented a lower efficiency in the interception in all the comparisons, *i.e.* always presented higher LAI for a relative similar radiation interception than durum wheat and a lower K, may play a role in favouring a relatively higher efficiency in radiation use for bread wheat cultivars, in most of the environments, as commonly those cultivars with small or more erectophyle leaves (attributes contributing to smaller coefficients of attenuation), can present a better distribution of light inside the canopy, increasing RUE, particularly in the case of the high yielding environments. This is in line with what was suggested by Duncan (1971) and supported by some experimental evidences (Angus *et al*., 1972; Innes and Blackwell, 1983).

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Chapter VII: General discussion

This general discussion intends to summarise the main results found in the different chapters, highlighting the main contributions made to knowledge and listing the main conclusions. In addition this Chapter does also suggest some future research themes which could be worthwhile pursuing.

1. Integrative discussion on the species differences in performance

Before starting the research work in this thesis, we were convinced that durum wheat was better performing under low-yielding conditions that bread wheat and the original idea at the onset of the project was simply to determine the physiological causes of that improved performance in such stressful conditions. The reason why we were persuaded of the better performance of durum wheat in low-yielding conditions was a compelling set of circumstances. Firstly, the relative small world area dedicated to durum is commonly restricted to semiarid conditions (Chapter I). Secondly the literature is abundant in comments of this nature: that durum wheat is more suitable for the drought prone environments *e.g.* (Percival, 1921; Bozzini, 1988; López-Castañeda and Richards, 1994; Trethowan *et al*., 2001; Elias and Manthey, 2005; Monneveux *et al*., 2012; Morris *et al*., 2015). Thirdly, there were cases in which durum was indicated as having some stress advantageous attributes (Marshal, 1987; Zhang and Oweis, 1999; Sairam *et al*., 2001; Reynolds *et al*., 2004; Wang *et al*., 2007; Dias *et al*., 2011). However, soon after starting the specific work and getting in a more in-depth contact with the literature, some questions emerged as many of the statements made in the literature were not based on experimental evidences, and in addition few works presented results conflicting with the generalised belief (Fisher and Maurer, 1978; Josephides, 1993; Zubaidi *et al*., 1999). It became clear sooner than later that there were limited cases of studies based on side by side field comparisons, and therefore data was scattered along papers, most of them based on experiments exploring a small range of environments.

This thesis contributes to this debate with a large number of side by side field comparisons of bread and durum wheat exploring a wide range of environments; as well as with a very extensive meta-analysis of the scattered data in the literature and a large dataset published by CIMMYT. Without pretending that this thesis ends the discussions and that conclusions are of universal value, the conclusions are based on an unprecedented large amount of conditions.

The main outcome of the work done, with either the database gathered from the literature or the results of the experimental work carried out, resulted in a clear crossover yield pattern in which, in contrast to the most widely accepted assumption, bread outyielded durum wheat under lower yielding conditions while durum wheat tended to present a higher yield potential. Furthermore, we found that the crossover yield pattern was also present in the dataset for the comparisons of biomass and HI.

After dividing the whole dataset gathered from the literature by the decade of release of the cultivars used in each study we found a likely explanation for the conflict between what has been traditionally assumed and facts revealed in this work. It seemed that durum breading pressure to improve yield potential started later, but at a higher rate of yield progress, in line with earlier comparisons of durum cultivars from different decades of releasing for the period (1967-1994), as pointed by Monneveux *et al.* (2005), in Pfeiffer *et al.* (1996) durum were increasing at *c.* 1.7 % year^{-1} in comparison with other comparisons for bread wheat, around the same period, (Calderini and Slafer, 1999) in which increases found where mostly below 1 % year^{-1}. In addition we confirmed, as earlier found by Pfeiffer *et al.* (2001) and Ammar from CIMMYT (personal communication, 2011) that the durum cultivars released in the last decades presented a relative higher yield potential than modern bread wheats. Presumably, the association between durum wheat and low yields could be originated at the early beginning of breeding, when the breeding effort over that species was much smaller. For instance, limiting the comparison of bread and durum wheat to cultivars released in the 60s, breads where superior in almost all comparisons. Furthermore, the relative increases in durum yield potential generated advantages for that species in the low, medium and high yielding conditions. Following that the crossover differences were not a mere effect of differences in breeding but a consequence of constitutive differences in their physiology; some other evidences go in that line, *e.g.* the fact that in the few comparisons of landraces from bread and durum wheat a similar crossover interaction (*e.g.* Karamanos *et al.*, 2008) or the fact that some of the constitutive differences determining the crossover differences in yield described in this thesis, *e.g.* kernel weight, tillering capacity, leaf size… have already been described for cultivated landraces and old cultivars of tretaploid and hexaploid wheat (Percival, 1921; Mac Key, 2005; Araus *et al.*, 2007). Furthermore, the association between durum wheat and stress resistance, not considering yield, could be a consequence of adaptation to the traditional environments where durum has been mostly cultivated, *i.e.* the Mediterranean Basin and other drought prone areas, as suggested by *e.g.* Mac Key (2005); Araus *et al.*, (2007). In particular, Moragues (2006) found that traditional durum landraces have suffered important morphological and physiological changes following their different paths of spreading along the Mediterranean basin, probably associated to climate differences. Indeed, we have identified in durum wheat some characters which could be potentially favourable to a relative better performance under stressful conditions; *e.g.* an earlier crop establishment, thicker stems which may likely remobilize a higher quantity of assimilates stored to grains; a root growing pattern which relative to bread wheat increased root production in the deeper layers for the drought prone conditions.

Nonetheless, most of these differences in response to the environment could be only a consequence of allometric scaling, and its usefulness for stress resistance should be further confirmed, *i.e.* the relative earlier crop establishment from durum, related to longer coleoptiles could be just be a simple effect of grain size more than a differential genetic response from the species for bread and durum wheat (Tretowan *et al*., 2001), and between durum wheat (Aparicio *et al*., 2002) as durum commonly generates heavier grains. The differences in the potential capacity for remobilization of biomass from stems to grains may be again an allometric scaling, for grain size and the relative longer time of grain filling from durum wheat, which will be in agreement with the relative higher sensitiveness of durum for post-anthesis drought Fisher and Maurer (1978), Sojka *et al*., (1981). The rooting differences may be the result of an alometric association with grain weight and tillering, *i.e.* a linear relationship has been found between the quantity of deeper seminal roots and grain size (Mac Key, 2005), while the number of derived adventitious roots are related to the number of tillers (Mac Key, 2005; Hockett, 1985). In that line bread wheat presented a lower K, a character theoretically related to leaf angle and eventually to higher radiation use efficiency, as a consequence of a better light distribution within the canopy.

The crossover differences in yield were a consequence of the relative number of grains per unit land area produced and contrastingly almost not related to differences in grain size. In addition, the differences were produced exclusively as differences in post-anthesis biomass, which was associated to an increase in the duration of biomass accumulation in GDD, and some photosynthesis activation in post-anthesis, detected as an interaction of NDVI for both species in the period. In addition, the differences in yield were highly related to some of the variables most determining sink-size already around anthesis, the spike dry weight at anthesis, the biomass generated around the period, and the total N absorbed at anthesis, which presented similar crossover interactions. Important associations between spike dry weight at anthesis and N content have already been found (Demontes-Mainard and Jeuffroy, 2004; Ferrante *et al*., 2012) and differences in biomass growth and partitioning and N content during that period have been already identified as the cause of differences in grain number and sink-strength in some experiments (*e.g.* Fischer, 1985; Prystupa *et al*., 2004; Reynolds *et al*., 2005).

As a summary, in the present study bread and durum wheat presented what could be qualified as two different strategies in yield formation, probably as a consequence of differences in the donor genomes (Ehdaie and Waines, 2013), because of ploidy (Mac Key, 2015; Araus, 2007) or as a consequence of differences in their particular selection and adaptation to the environment (Moragues, 2006; Araus, 2007). Under low yielding conditions the strategy of producing a relative higher number of structures was positive to generate sink, while under a context of high resource availability and higher generation of reproductive structures, the relatively lower rate in the generation of structures was more efficient in generating sink and yield. To understand how sink advantages in the high yielding conditions may occur, we can revisit the theoretical ideotype for a high potential yielding cultivar, proposed long time ago by Donald (1968), in which the more "communal" plants would enhance yield by transferring the resources used in competition between plants of a crop to grains, mainly because of competition with light since density of stems and leaves is very high in that situation; some advantages for yield potential have already reported to be related with communalism (Reynolds *et al*., 1994). However, under a context of restricted nutrition to reduce tillering may be counterproductive as the number of stems produced is a coarse regulation for plants to adapt to the environments (Slafer *et al*., 2014), and a low number of them may reduce the possibility to adapt to the post-anthesis conditions which may be detrimental of yield on most of the situations. Actually that was the case in our exp. 1 which was rather dry until anthesis when important rains felt, which is common situation under the erratic rains of the Mediterranean climate; in that line, increasing sowing density for durum in comparison to bread has been a common intuitive practice of Australian growers to overcome the tillering problem (Zubaidi *et al*., 1999) and increasing the number of spikes per m^{-2} has already been object of breeding (Pfeiffer *et al*., 1996; Royo *et al*., 2007). However, in addition to the gap in the number of spikes by surface produced, the degree of competition inside every culm between the growing stem and spike, must have been higher for that particular situation for the durum wheat with thicker stems (Fig. 1), and possibly because of competition a negative relationship between the relative weight per stem and per spike at anthesis was found, decreasing more markedly the partition to spike.

Regarding the capacity to predict yield and biomass at some early stages of wheat development the present thesis confirmed the capability of the spectral reflectance indexes like NDVI to produce reasonably good assessments at early stages as the moment of terminal spikelet. This capacity had been acknowledged when determinations were made later, as previously discussed by Babar *et al*. (2006), for bread wheat, and by Aparicio *et al*. (2002), for durum wheat. Identifying this capacity of NDVI at earlier stages is relevant as it may help farmers to decide on management practices (*e.g*. N fertilization) timely. In addition, good estimations of the photosynthetic performance were found in post-anthesis, which significantly captured the variations between both species up until almost maturity, as proven by Lopes and Reynolds (2012). After anthesis leaf senescence makes particularly tedious achieving good readings of radiation interception, and spectral indices could be a reliable alternative; thought it is worth to mention that saturation of the NDVI index around anthesis was a problem to detect the species variability under particularly high yielding conditions.

Finally, it is worth to mention some other minor issues which could be the object of future experiments to confirm these results. That was the case for the relatively higher instability of durum grain weight, already discussed or present in some experimental comparisons (*e.g.*: Corbellini *et al.*, 1997; Modhej *et al.*, 2008; Dias and Lidon, 2009; Zubaidi *et al.*, 1999; Cossani *et al.*, 2011); despite that within this thesis the effect of grain weight variability on yield was minor; as discussed in Chapter III, in the relatively temperature-mild years, bread grain weight along the treatments was almost invariable in comparison to durum, which changed greatly, this was in contrast with the particular year of exp.2, where temperatures were high around anthesis, and under those particularly stressed conditions, bread and durum wheat changed grain weight similarly; this could be in line with Reynolds *et al.* (2004) who found a group of durum cultivars adapted to warmer conditions around grain set, and should be further studied the reasons of the durum higher grain instability under mild temperature conditions. It is worth to mention that the fertilized treatments presented the smallest grain weight in the exp. 2 which could be in line to a major grain reduction produced by the combination of N and temperatures (Zahedi *et al.*, 2004; Passarela *et al.*, 2008; Ordoñez *et al.*, 2015).

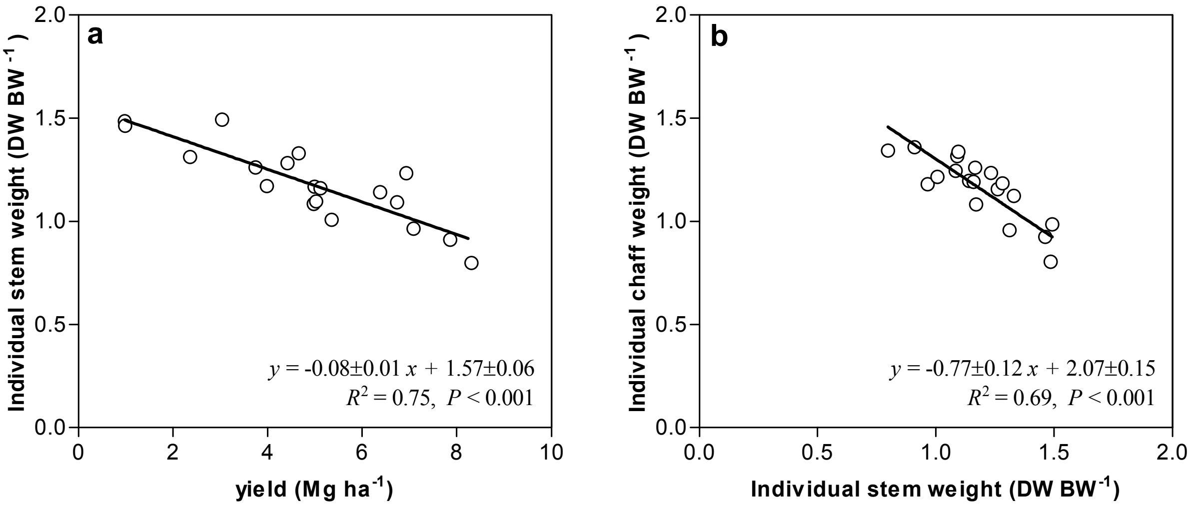

Figure 1. Relationship between the bread and durum wheat ratio for the individual stem weight (durum bread^{-1}) and the average yield of the environment a) and between the bread and durum wheat ratio for the individual chaff weight and the individual stem weight b).

Naturally, the differences in yield were related to differences in the efficiency in the use of the resources, and clear interactions with the environment potential were presented for the RUE, WUE and NUE. Nonetheless is interesting to comment about some small effects *e.g.* breads RUE particularly in pre-anthesis was higher in most of environments, could that be related to differences in the size or the angle of leaves insertion? While regarding the water use in most of comparisons durum consumed for our experiments slightly higher amounts of water in most of comparisons, could those differences be related to differences in root production? Or regarding the N economy it is worth to mention that differences in yield barely affected the relative grain concentration, varying little along the environments, could be that differences in N concentration constitutive?

2. Future research based on the results found in the present thesis.

Here I present some opportunities for future research, based in the results of the present thesis, which I believe could be worthwhile to pursue.

-Under drought prone conditions durum lower yield was associated with its lower number of stems; however, it will be worth to carry out experiments modifying the sowing rate to determine quantitatively to what degree this genotypic inconvenience may be solved agronomically or whether breeding shall focus on improving tillering capacity in durum wheat. Carrying out this sort of studies would also help to further improve the knowledge about the nature of likely compensations between the different yield components.

-The apparently higher grain instability from durum in comparison to bread wheat, reported in the present thesis, may also deserve further studies to determine whether the lower stability might be related to the constitutively lower fruiting efficiency, and not particularly with the high temperatures of exp.2. However, it will be worth to study in further detail, the regulation of sink size and the response to temperature treatments of contrasting experiments.

-Although it was not an aim of the work, and therefore we did not impose treatments required to conclude on likely interactions between N and heat, we found a possible association between N treatments and high temperatures which could be worthwhile to explore in future work, as it may imply changes in N management if it may alter sensitivity to stress (as it seems to be the case in other cereals).

-One of the secondary results from this thesis was a differential in the apparent remobilization of stem weight to grains between the species, particularly under high yielding conditions: it would be convenient to quantify these amounts of potentially remobilizable reserves and potential demand unsatisfied by current photosynthesis (with direct determinations of the water soluble carbohydrates). This would shed light on the importance (or otherwise) of high levels of reserves stored in the stems before anthesis (which otherwise might be used in setting a stronger sink capacity).

-In this thesis a differential in the root growth response with the irrigation treatments was found. It would be worth to uncover to what degree the differences in root systems are genuinely due to genetic differences related directly to those traits or are merely the outcome of an indirect effect given by constitutive differences between both wheat types in seed size and/or in tillering capacity.

3. Conclusions

1- The traditional land distribution which prioritizes durum relative to bread wheat in the stressed lower yielding environments, particularly in the Mediterranean basin, is not justified in the light of this thesis results. In our experiments, as well as in the extended literature database meta-analysed, there were no evidences to support that durum wheat possess any general yield advantage over bread wheat on those low-yielding conditions.

2- Under high yielding conditions, the assumption that bread wheat would present higher yields (and that is why in regions where both are grown bread wheat is commonly allocated higher-yielding conditions), was not supported either by the present thesis which oppositely found durum to possess higher yield potential than bread wheat.

3- Although durum has constitutively both lower grain number and higher grain weight than bread wheat due to its constitutive lower fruiting efficiency, both species reacted similarly to the availability of resources by generating more grains the gap in the number of grains between the species and it relative numerical importance was the main factor regulating the differences in yield.

4- Radiation, water and N use efficiencies naturally widely varied across the experimental environmental range and were similar for both species. However, in line with the previous conclusions, as a consequence of the environmental differences in yield; the species relationships in the efficiency in the use of the resources were crossover with the yielding environment.

5-Both wheat species adjusted yield mainly by regulating the amount of grains generated at anthesis, despite that, durum changed grain size more markedly than bread wheat (that barely changed the average grain weight). That higher degree of variation was most likely associated with a regulation of sink size and contrastingly when grain potential size was affected by high temperatures both species changed grains size similarly.

6-Based in the acceptable correlation between the NDVI index at early stages of development and yield, it would be possible to realize good assessments of yield expectations from early stages of development and then use NDVI at these early stages as an additional diagnosis tool for accurate nutrient management.

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Annex I: Can wheat yield and its differences be assessed by early measurements of Normalized Difference Vegetation Index (NDVI)

Abstract

An early prediction of crop biomass at maturity and yield is important in different circumstances. The use of spectral reflectance indices, such as the Normalized Difference Vegetation Index (NDVI), has been proposed as a fast, nondestructive way of estimating crop growth capacity. In this study, we examined whether NDVI assessment relatively early in the crop cycle may be useful for predicting final biomass and yield in wheat. To that end, NDVI was measured and biomass quantified regularly from tillering to maturity for six different wheat genotypes grown under a contrasting range of N and water availabilities. In addition, final biomass and yield were measured at maturity. In line with expectations from the literature, we found that NDVI at milk grain stage was well correlated to final yield and biomass. However, it was also observed that NDVI at the onset of stem elongation was also reasonably correlated to both attributes. Because crop growth in wheat from the end of tillering to anthesis is related to the determination of grain number and yield, we propose the use of NDVI at the onset of stem elongation as a complementary criterion for establishing the required late crop management (N fertilisation, irrigation) practices.

Keywords: Biomass assessment; grain yield; Mediterranean conditions; NDVI; wheat.

1. Introduction

Estimates of crop biomass and related traits [such as the leaf area index (LAI)], as well as yield, are frequently required. For instance, in large breeding programmes, non-destructive biomass estimations may be useful in selection, particularly if they are quick, cheap and easy to perform. In crop management, reliable biomass estimations relatively early in the growing season, when crop yield may still improve in response to increased availability of resources (*e.g*. Nfertilisation), may allow decisions to be made regarding the need for additional inputs. Spectral reflectance indices (SRI) can be correlated to biomass and LAI, among other traits. One of the most widely used SRI is the Normalized Difference Vegetation Index (NDVI), which relates the difference between near infrared reflectance and red wavelength reflectance with the reflectance of both wavelengths. In fact, NDVI has been proposed as a means of estimating biomass, LAI, photosynthesis or yield in wheat and other cereals (e.g. Fernández *et al*., 1994; Filella *et al*., 1995; Aparicio *et al*., 2000; Bort *et al*., 2002, 2005; Royo *et al*., 2003), mainly based on the different patterns of reflection of green organs and soil.

Most of these assessments using spectroradiometric indices have been performed in the last part of the crop cycle (for cereals, usually after anthesis). Thus, for example, measurements of NDVI in wheat at the milky-grain stage seem to be more closely correlated to yield than earlier measurements (Royo *et al*., 2003). Although there is abundant literature on the relationships between biomass and NDVI (or other SRI) measured simultaneously, to the best of our knowledge, there is far less information on the use of NDVI in relatively early stages to predict final biomass or yield.

An early prediction of the potential biomass and yield of a given crop at maturity may be particularly relevant to both breeding and management. Specifically, much of the yielding capacity of a wheat crop is related to growth during a few weeks before anthesis (Fischer, 1985; Slafer, 2003). Thus, there is a functional basis for the hypothesis that relatively early (say, by the onset of stem elongation) measurements of NDVI may serve to predict final biomass and yield and may consequently become a tool for deciding on management options at that stage. We then aimed to measure NDVI and biomass from before the onset of stem elongation to maturity in order to determine whether a relatively early NDVI assessment may provide a good estimation of final biomass and yield. For this purpose, we quantified NDVI and biomass regularly in six different wheat genotypes grown under a wide range of N and water availabilities.

2. Materials and methods

A field experiment was carried out during the 2004-05 growing season in the Mediterranean location of Agramunt, Lleida, Spain. The experiment was sown on 16 November 2004, at a rate of 250 viable seeds m^{-2}. Weeds and diseases were controlled using agrochemicals following manufacturer's recommendations for application.

Treatments consisted of the factorial combination of six genotypes, two levels of N availability and two levels of irrigation. Genotypes consisted of three durum wheat (*Triticum turgidum* L. var. *durum*) cultivars (Simeto, Claudio and Vitron) and three bread wheat (*Triticum aestivum* L.) cultivars (Anza, Soissons and Provinciale). These were chosen because of their wide cultivation in the region and/or good behaviour in previous studies. The two levels of N availability were an unfertilised control and a fertilisation that provided unlimited N availability (200 kg N ha^{-1} with NH_4NO_3, applied after emergence, 49 days after sowing). The two levels of water availability were a rainfed and a drip-irrigated treatment, irrigating from early spring on a weekly basis. Total rainfall was 181 mm, and irrigated plots received a further 180 mm.

The experimental design was a split-block split-plot, with three replications: the main plots were the combination of genotypes and irrigation levels, while the subplots were N levels. The size of the experimental units (subplots) was 12 m^2, with 17 rows sown 18 cm apart.

Canopy reflectance was measured and NDVI calculated using a portable spectroradiometer (Greenseeker Hand Held^{TM} optical sensor unit, model 505; NTech Industries, Inc., Ukiah, CA, USA). Measurements were taken around midday on sunny days by passing the sensor over the subplots at a height of approximately 0.40–0.60 m above the canopy. Each subplot was also sampled (50 cm from a row located in a representative zone) for biomass determination, and dry weight was measured after drying the samples at 70ºC for 3 days. Both NDVI and biomass were measured on a weekly basis, from 22 March (plants at tillering stage) to 24 June (plants at late grain filling). In addition, yield and final biomass were determined at maturity (100 cm from a row). Crop growth during stem elongation was calculated as the difference between biomass at anthesis and at jointing.

3. Results and discussion

The contrasting conditions given by the combination of the different N and water regimens assayed produced a wide range of both biomass (~1–10 mg ha^{-1}) and yield (~0.2–5 mg ha^{-1}) at maturity (Table 1). Thus, although the study comprised a single year, the range of environmental conditions explored was substantial. The cropping season was very dry, with rainfall below average values. This was quite beneficial in the context of the study, as with the irrigation treatments, we were able to expand the range of conditions explored in the study, covering water availabilities from a dry to a wet year, as reflected by the range in biomass and yield mentioned previously). Because of this particular situation, water availability, mainly depending on the irrigation schedule, accounted for most of the variability in yield and final biomass, as well as in NDVI for most of the dates when it was measured. However, the effect of nitrogen treatments, both directly and in interaction with irrigation, was significant for both yield and final biomass, as well as for measurements of NDVI. Differences between the genotypes were found only for yield and final biomass but not for NDVI measurement. The effect of the other interactions was minor in the total amount of variation of the different parameters.

Consistent with the findings of Babar *et al*. (2006a,b), NDVI values steadily increased until the beginning of grain filling, with the highest values of NDVI observed around the starting of the milky-grain stage (182 days after sowing) and then decreasing until maturity. There was a strong positive relationship between biomass and yield (Fig. 1). The close link between these two elements is consistent with what can be expected when yield is dependent on the availability of resources (Fischer, 1993). A good relationship between yield and total biomass is mandatory for a system intended to predict yield early in the season by assessing the growth capacity of the canopy.

NDVI at early grain filling (i.e. milky stage) was strongly positively correlated to biomass and yield at maturity (Fig. 2). In addition, both wheat species exhibited similar trends ($r_{\text{biomass–NDVI milky stage}} = 0.72$ and 0.77 and $r_{\text{yield–NDVI milky stage}} = 0.68$ and 0.79

Table 1 Means for yield, biomass and NDVI measured from late tillering (126 days after sowing) until immediately before maturity (210 days after sowing), from two species of wheat (bread and durum wheat) for each of the two levels from the two treatments: irrigation (rainfed and irrigated) and nitrogen fertilisation (0 kg ha^{-1} or 200 kg ha^{-1} of fertiliser)[a]

		Bread Wheat				Durum Wheat																
		Rainfeed		Irrigated		Rainfeed		Irrigated		Genotype	Irrigation	Nitrogen										
		N0	N200	N0	N200	N0	N200	N0	N200	(G)	(I)	(N)	Rep	G × Rep	I × Rep	I × G × Rep	I × N	N × G	I × G	I × N × G	Error
Yield		1316	1271	2669	3179	782	679	1892	2536	10.94*	55.44*	1.44*	3.10**	5.31ns	1.13ns	8.71**	2.42**	2.39ns	0.96ns	1.58ns	6.51
Biomass		2743	2974	5372	6757	2127	2068	4117	5930	7.92**	54.46***	4.11**	2.63*	5.86ns	0.82ns	8.80*	3.31**	1.52ns	0.85ns	1.58ns	8.09
NDVI (days from sowing)	126	0.16	0.15	0.20	0.18	0.15	0.15	0.19	0.19	10.80ns	30.35ns	0.97ns	2.34ns	10.72ns	6.12ns	5.13ns	0.17ns	4.38ns	4.90ns	1.26ns	22.80
	141	0.18	0.15	0.32	0.31	0.17	0.17	0.30	0.33	1.49ns	48.99ns	0.00ns	14.29**	5.61ns	9.02**	3.93ns	0.18ns	1.04ns	0.79ns	0.81ns	13.79
	147	0.18	0.15	0.32	0.31	0.17	0.17	0.30	0.33	1.49ns	48.99ns	0.00ns	14.29**	5.61ns	9.02**	3.93ns	0.18ns	1.04ns	0.79ns	0.81ns	13.79
	154	0.17	0.17	0.33	0.41	0.19	0.16	0.36	0.37	9.13ns	53.22*	0.33ns	3.78*	8.32ns	2.53ns	3.04ns	1.32ns	1.06ns	5.58*	0.64ns	11.01
	168	0.19	0.20	0.30	0.50	0.19	0.20	0.37	0.57	2.06ns	51.74**	9.60***	2.56*	7.00*	0.94ns	4.68ns	8.38***	0.15ns	6.14ns	0.27ns	6.43
	175	0.20	0.19	0.37	0.52	0.18	0.20	0.39	0.58	1.92ns	65.49*	7.05***	2.26**	6.18**	1.37*	3.80*	6.15***	0.45ns	1.80ns	0.30ns	3.17
	182	0.28	0.29	0.47	0.55	0.25	0.26	0.42	0.61	4.08ns	57.53*	5.41**	4.51**	6.60*	1.64ns	5.55ns	3.83**	0.72ns	2.77ns	1.13ns	6.18
	189	0.21	0.21	0.40	0.51	0.17	0.17	0.34	0.49	3.61ns	61.24*	3.96**	1.16ns	8.17**	1.80*	6.19*	3.52**	0.24ns	4.27ns	0.46ns	5.32
	196	0.17	0.17	0.33	0.44	0.16	0.16	0.29	0.40	3.38ns	53.96*	4.57**	3.29*	9.48*	1.67ns	7.65ns	3.90**	0.57ns	2.25ns	0.74ns	8.46
	203	0.14	0.15	0.32	0.37	0.13	0.14	0.22	0.33	9.59ns	50.23*	3.27**	0.00ns	5.78ns	1.84ns	7.10ns	1.68*	1.27ns	8.91ns	2.31ns	7.98
	210	0.13	0.18	0.13	0.21	0.14	0.20	0.13	0.23	4.43ns	0.92ns	34.97***	1.41ns	8.05ns	6.71*	7.68ns	2.39ns	1.82ns	3.13ns	4.98ns	23.46

ANOVA, analysis of variance; NDVI, Normalized Difference Vegetation Index; ns, not significant; Rep, replications.

[a]The different effects from the ANOVA model are shown as a percentage of the sum of squares.

ns >0.05; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

for bread and durum wheat, respectively). Positive correlations between NDVI measured during the last part of the crop cycle (i.e. from heading/anthesis onwards) and yield have already been reported in bread (Babar *et al.*, 2006a,b) and durum wheat (Aparicio *et al.*, 2000; Royo *et al.*, 2003; Bort *et al.*, 2005). Overall, these studies show a clear trend: associations of biomass and grain yield with NDVI measured during grain filling and even with NVDI measured at heading are greater than those recorded at booting.

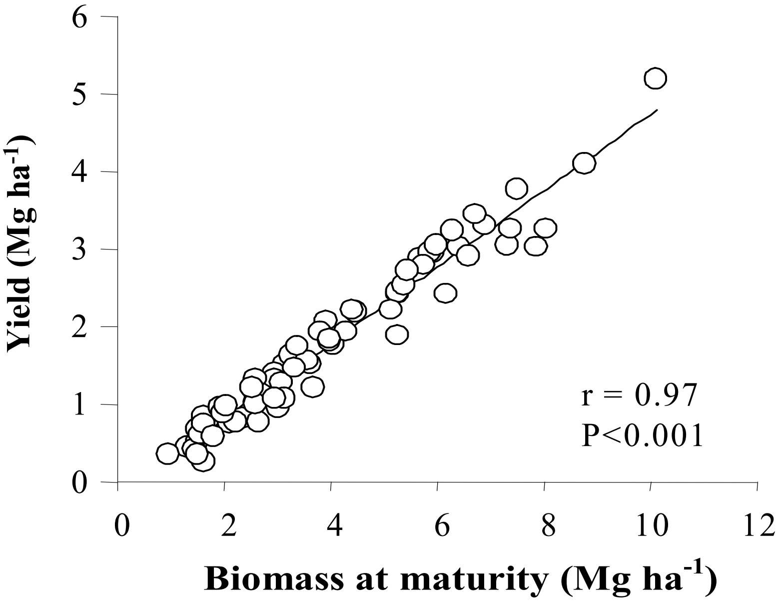

Figure 1. Relationship between biomass at maturity and grain yield for a wide range of yielding conditions given by six wheat genotypes grown under a factorial combination of two (low and high) nitrogen and water availabilities.

Consequently, and in agreement with previous literature, NDVI seemed to perform reasonably well in estimating yield if NDVI differences between treatments were assessed at the beginning of the effective period of grain filling, 2 weeks after anthesis.

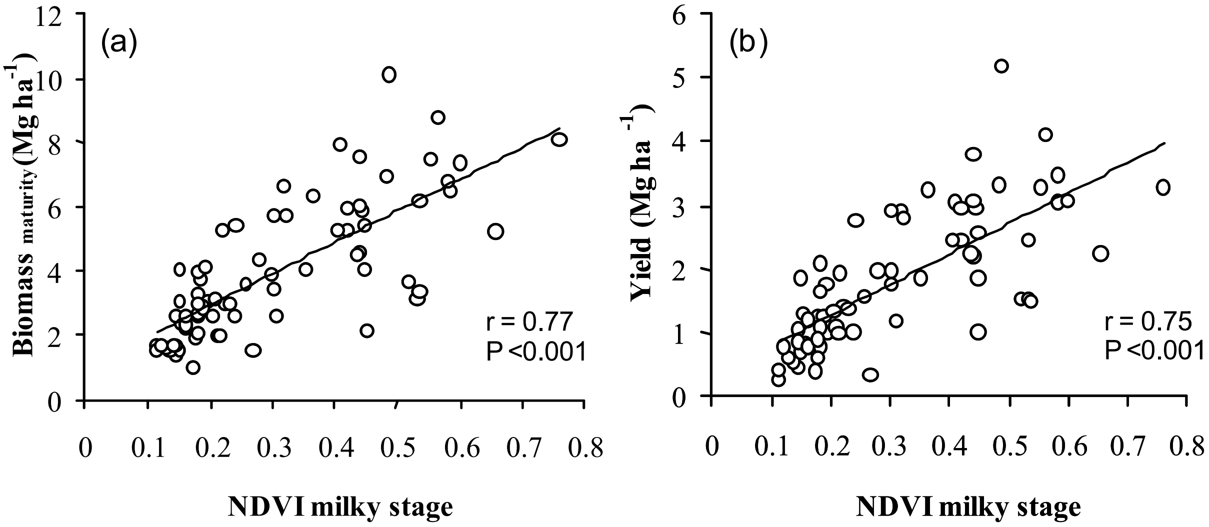

Figure 2. Relationship between NDVI at the milky stage of grain filling (~14 days after anthesis) and (a) biomass at maturity and (b) grain yield. NDVI, Normalized Difference Vegetation Index.

The question is whether measurements of NDVI taken up much earlier during the crop cycle, when there is still a chance of preventing low yields caused by a lack of available resources, can still predict final biomass at maturity and yield. Fig. 3 shows the correlation coefficients of the relationships between biomass and yield at maturity against either NDVI or biomass measured at different moments during the crop cycle. Although biomass at maturity and yield was best explained (i.e. they showed the highest value of *r*) by NDVI measurements made at, or shortly after, anthesis, fairly significant correlations were still found with NDVI measurements made much earlier, including measurements corresponding to the onset of stem elongation ($r = 0.58$, $P < 0.001$; Fig. 3). The same trend was observed for both wheat species. Moreover, results show that NDVI assess yield and biomass at maturity better than biomass measured in the crop stages before anthesis. The higher capacity to discriminate growth potential by NDVI compared with biomass could be the consequence of the high ratio green area/biomass in the early crop stages and/or the higher capacity to make a representative sample from this method.

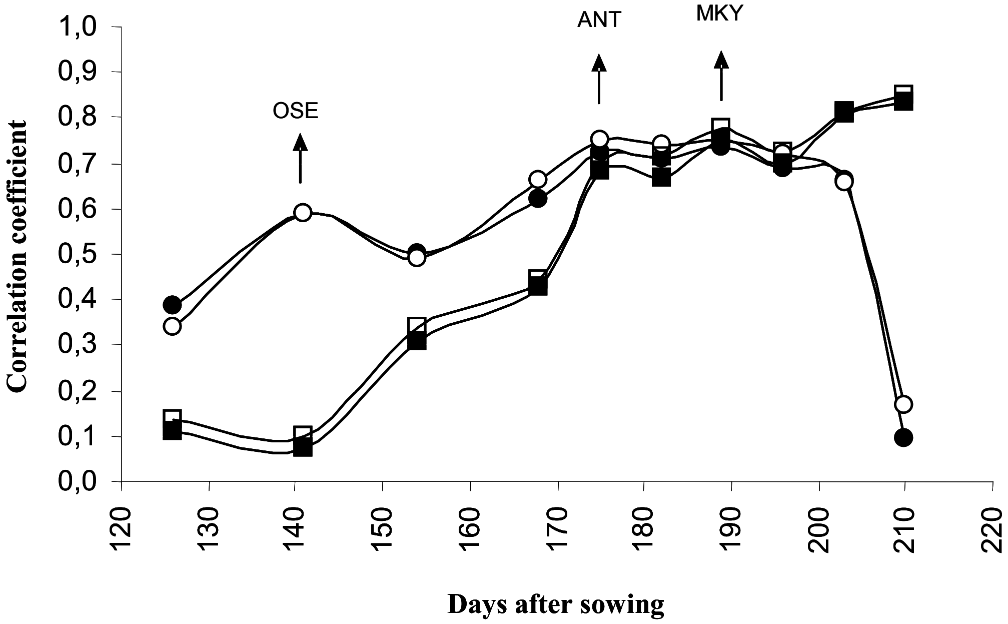

Figure 3.Correlation coefficients of the linear regression of NDVI (circles) and biomass (squares) measurements taken at different stages of the crop cycle against either grain yield (closed symbols) or biomass at maturity (open symbols) (n = 72; r > 0.38 is significant at $P < 0.001$). NDVI and biomass were measured from late tillering (126 days after sowing) until immediately before maturity. ANT, anthesis stage; MKY, milky grain stage; NDVI, Normalized Difference Vegetation Index; OSE, onset of stem elongation.

The ability to predict final biomass at maturity and yield from measurements made at the onset of stem elongation may be relevant for the management of N fertilisation and irrigation as crop responsiveness seems to be still largely maintained by the onset of stem elongation (Fischer, 1993). Thus, NDVI measured at this stage may be a complementary tool used for determining the likely response to a fertilisation rate applied.

It is highly likely that the overall correlation between yield and NDVI at the onset of stem elongation is mediated by the ability of this measurement to estimate growth during stem elongation (Fig. 4a), which in turn largely determines yield in wheat (Fig. 4b).

It has been well established in the literature that wheat yield is strongly correlated to the number of grains per unit land area and that this component is strongly dependent on crop growth during the stem elongation period (see Slafer *et al.*, 2005 and references therein).

Therefore, estimating differences in canopy development at the onset of stem elongation using NDVI measurements may reliably anticipate growth capacity during the following few weeks, in turn largely affecting yield.

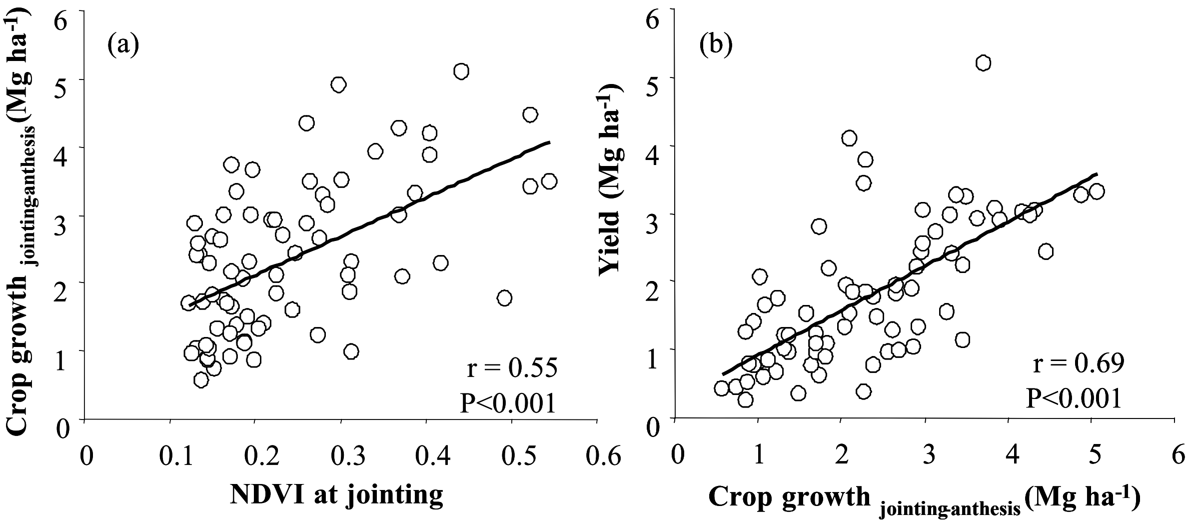

Figure 4. Relationships between biomass accumulation between the onset of stem elongation (jointing) and anthesis and NDVI at the onset of stem elongation (a) and crop yield and biomass accumulation during stem elongation (b). NDVI, Normalized Difference Vegetation Index.

If the NDVI is to be used in the general forecasting of biomass and yield, it is important to consider the variable ratio between green biomass and total biomass, which constantly changes throughout the season and decreases until near maturity. Thus, the strength and the slope of the relationship between NDVI and simultaneously measured biomass increased during the crop cycle (Fig. 5), with the highest correlation coefficients recorded around the milky stage and the highest slope of the relationship observed near maturity.

In contrast, NDVI measurements taken between anthesis and milky stage are the best estimates of yield and final biomass, compared with other developmental stages. Our results showed the difficulty in assessing the predictive value of NDVI depending on the developmental stages, as previously discussed by Babar *et al.* (2006b), for bread wheat, and by Aparicio *et al.* (2002), for durum wheat.

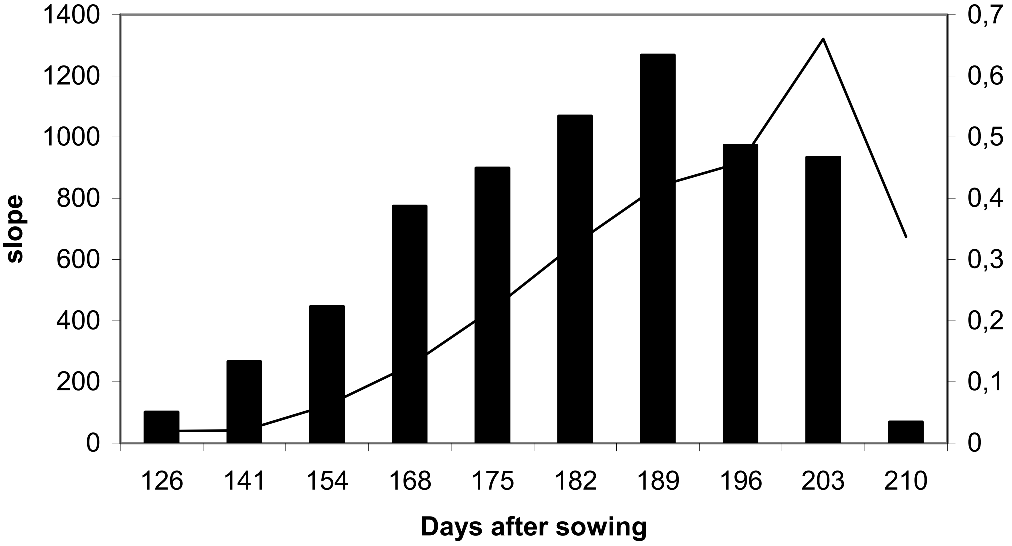

Figure 5. Slope (line) and r2 (bars) from the linear regressions of NDVI and biomass measured the same day. NDVI was measured from late tillering (126 days after sowing) until immediately before maturity. NDVI, Normalized Difference Vegetation Index.

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